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CONTRIBUTIONS TO OCEANOGRAPHY AND FISHERIES BIOLOGY

CAPE TOWN
1970

Republic of South Africa
Department of Industries
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CHLOROPHYLL IN THE SEA OFF SOUTH AFRICA

H. HOY

The determination of plankton pigments in sea-water by spectrophotometric analysis is widely employed. The method has been described by Richards (1952) and modified by Creitz & Richards (1955) and Strickland & Parsons (1960, 1965).

To obtain a guide to the relative abundance of phytoplankton and also to determine chlorophyll variations, the routine measurement of chlorophyll in sea-water was started in 1965. During the following year the investigation was also extended to the determination of chlorophyll in phytoplankton from N50V net samples.

Sea-water samples were collected from a set of fourteen Stations occupied once every month (Shannon 1966). Eight of these Stations were off the South Coast between St. Sebastian Bay and the Cape of Good Hope, with four Stations (80-1, 72-1, 60-1 and 52-1) inshore and another four Stations (80-5, 72-5, 60-5 and 52-5) offshore. The remaining six Stations were situated off the West Coast between Cape Point and St. Helena Bay and consisted of three inshore (44-1, 36-1 and 24-1.5). The inshore and offshore Stations were situated respectively five and eighty-five miles from the coast (Fig. 1). Sea-water samples were collected inshore at the surface and at 10m but offshore at the surface only. All surface samples were collected by means of a plastic bucket whereas the 10m samples were taken with a Nansen-Pettersson sampling bottle.

The N50V net samples for chlorophyll determinations were selected at random at stations in the area between St. Sebastian Bay and St. Helena Bay. The net was hauled vertically between 50m and the surface.

It is well known that the use of chlorophyll as an index of phytoplankton abundance has a distinct disadvantage since the variation in chlorophyll content according to species cannot usually be taken into account. However, the chlorophyll concentration in filtered sea-water does give a useful indication of productivity.

METHODS

The analytical method of determining the chlorophyll was that outlined by Strickland & Parsons which was based on the procedure of Richards. As filtration facilities were not always available on both the research ships of the Division, the sea-water samples had to be stored in polythene bottles at approximately -15°C from one to ten days before filtration. Whenever a sample was filtered on board the filter paper was stored in a desiccator containing silica gel, at approximately -15° for one to twenty days before extraction. During filtration a vacuum of 50 cm Hg was maintained.

Millipore HA, 47 mm, white, plain filters were used and about 0.1g $MgCO_3$ was added during filtration. The volume of filtered sea-water varied from 500 ml to 3 l. according to the quantity of suspended material present.

The filter was extracted in a graduated stoppered glass centrifuge tube, made up to 10 ml with 90% acetone, and left for ± 20 hours to extract. If the extract was still turbid after centrifuging at 4,000 r.p.m. for 10 minutes, a few drops of pure acetone were added and the extract again centrifuged. The volume of the extract was then read to the nearest 0.1 ml and the extinction read in a Unicam SP600 spectrophotometer at 750, 663, 645 and 630 $m\mu$. One or four centimeter cuvettes were used depending on the colour intensity of the extract. Pure 90% acetone was used as blank, as Creitz & Richards (1955) found that a filter dissolved in 90% acetone caused no interference. The extinction at 750 $m\mu$ was used as being characteristic for turbidity and all the other extinctions were corrected accordingly.

The chlorophyll amounts were calculated by means of the equations developed by the SCOR-UNESCO Working Group in 1964.

In order to investigate the possible correlation between chlorophyll content and phytoplankton settled volumes, several N50V net samples were collected. Each sample was divided into two parts. The one portion was preserved with formalin and subsequently filtered through 350 micron mesh netting to remove any zooplankton. After allowing to stand in measuring-cylinders for 24 hours, the settled phytoplankton volume was measured. The other portion was stored in a polythene bottle at -15°C. This frozen sample was defrosted and, after the removal of zooplankton by means of a 350 micron mesh net, was filtered through a millipore HA filter. This filter was stored and extracted as previously explained.

Whenever a water sample was taken at 10m for chlorophyll estimation, an additional sample was collected for determining total phytoplankton count in accordance with the method described by de Jager (1957).

Dissolved oxygen was determined by the Winkler method (Mostert 1966).

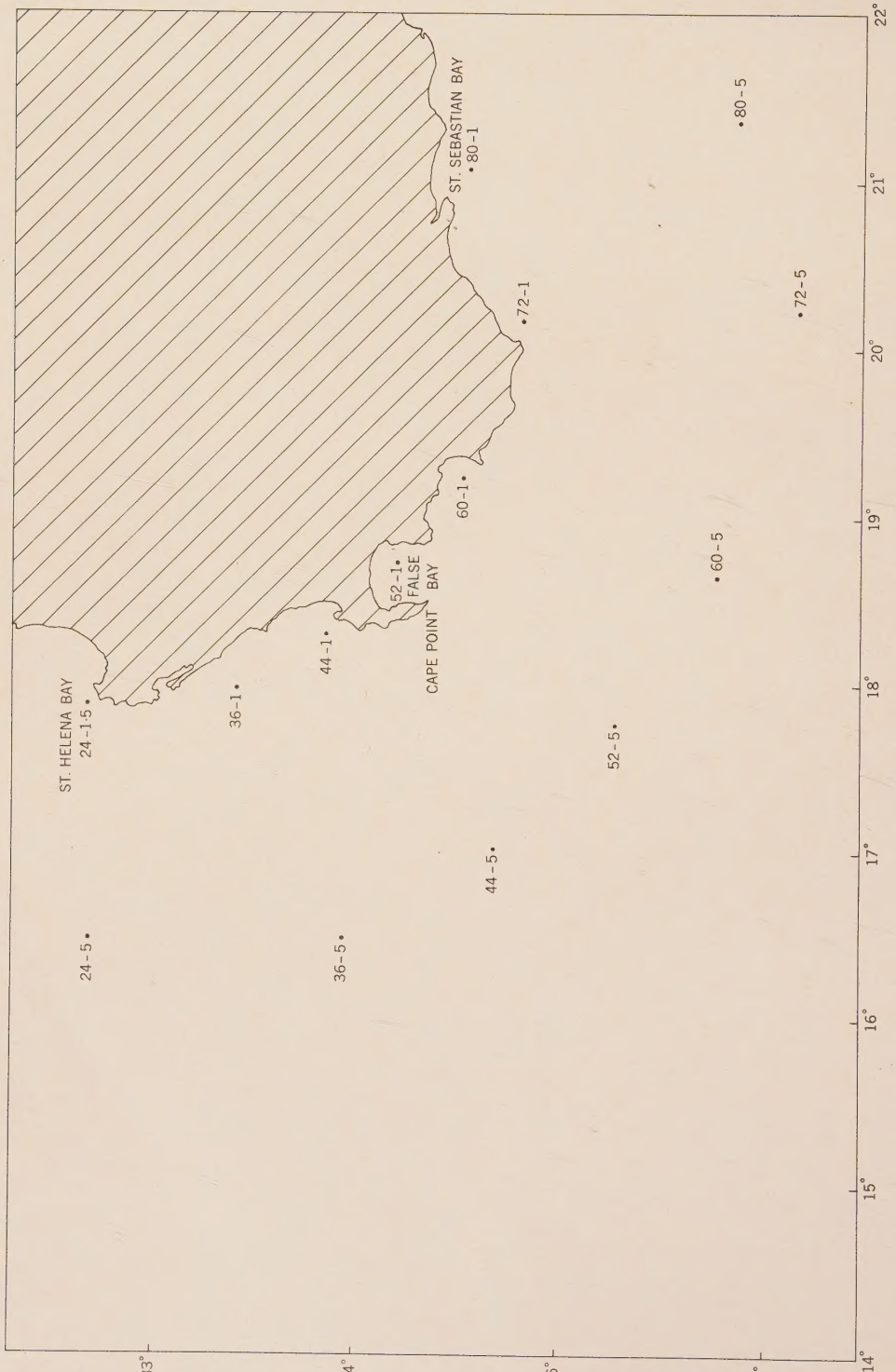

FIG. 1. POSITION OF SAMPLING STATIONS

Trigsurvey 1969.

RESULTS

The chlorophyll and dissolved oxygen contents of sea-water samples are presented in Table I. Table II compares the results of the chlorophyll determinations and the settled volumes of the N50V net samples.

The relative standard deviation was determined for chlorophyll *a*, *b* and *c* on 500 ml aliquots. The relative standard deviation for chlorophyll *a* at the 7 μg level was found to be 8%, for chlorophyll *b* at the 1.5 μg level it was 19% and for chlorophyll *c* at the 4 μg level it was 21% using a 4 cm pathlength cuvette. All work had to be done in 4 cm cuvettes which could partly explain the high relative standard deviation.

DISCUSSION

TOTAL CHLOROPHYLL CONTENT AND PHYTOPLANKTON COUNT

The only data available for the comparison of total chlorophyll content and diatom counts were those from two Stations, namely;

Station 24-1.5

Moderate amounts of chlorophyll were recorded for February, March and April 1965, yet in all three cases the count did not exceed 1 x 10^5 cells per litre (Fig. 2). In May 1965 an exceedingly large number of cells were recorded, but the chlorophyll content was less than in February, March or April of the same year. The only months where the two parameters followed a similar trend was in September and October 1965 and April, May and June 1966. It appears that phytoplankton counts and chlorophyll content are not necessarily related and can not be represented as a constant ratio, because of the variable chlorophyll content per cell in the different species.

During May 1965 the dominant species was *Asterionella japonica* whereas during the months of February, March, April and June of the same year species having much larger chromatophores predominated. It is evident that, in the above case, cell counts will not give a true indication of chlorophyll concentration. This may account for the low chlorophyll recorded during May in spite of the relatively large number of cells present.

In September and October 1965 the chlorophyll content and the phytoplankton count followed the same trend, that is a decrease in the phytoplankton count from September to October, was accompanied by a decrease in the chlorophyll content. The most abundant species in these samples were of a similar size.

From Figure 2 it can be seen that a large number of cells were present in March 1966. These were small in size (± 500 μ^3), however, and the corresponding amount of chlorophyll recorded was low.

In April, May and June 1966 the chlorophyll concentration and the cell counts followed similar patterns. In the phytoplankton found during March 1966 *Chaetoceros socialis*, a small cell (± 500 μ^3), predominated, whereas in April 1966 the bulk of the sample was composed of *Asterionella japonica*. The latter is also a small cell (603 μ^3) yet its chromatophores are relatively large, which possibly explains the exceptionally high chlorophyll content. The low chlorophyll concentration in May 1965 when the predominant species was also *Asterionella japonica*, however, contradicts this argument. Another anomaly is the fact that in the sample collected during May 1966, although no identifiable phytoplankton was present, chlorophyll was detected. In June 1966 the phytoplankton species were mainly small and a low chlorophyll concentration was recorded.

It can be concluded, therefore, that there are factors other than the species type which influence the quantity of chlorophyll present in sea-water.

Station 52-1

As at Station 24-1.5, the ratio between total chlorophyll concentration and phytoplankton count was not constant. Most discrepancies could be explained by the characteristics of the species present.

The predominant species in the samples of February and May 1965 were of a small size and consequently the amount of chlorophyll present was low (Fig. 3). The most abundant species found in March, April, June, July and August 1965 were larger than those found in February and May 1965 and hence the amount of chlorophyll relative to the number of diatoms was higher.

In September 1965 *Asterionella japonica* predominated and a high chlorophyll content was recorded. The sample for October 1965 was composed mainly of large diatoms and the chlorophyll concentration was high despite the low cell count.

The discrepancies recorded during the period February to June 1966 could also be explained on the basis of species composition.

From the above it is clear that it is impossible to make a direct comparison between the chlorophyll concentration and the number of cells present, unless the species and its chromatophore size as well as the prevailing oceanographic conditions are taken into account.

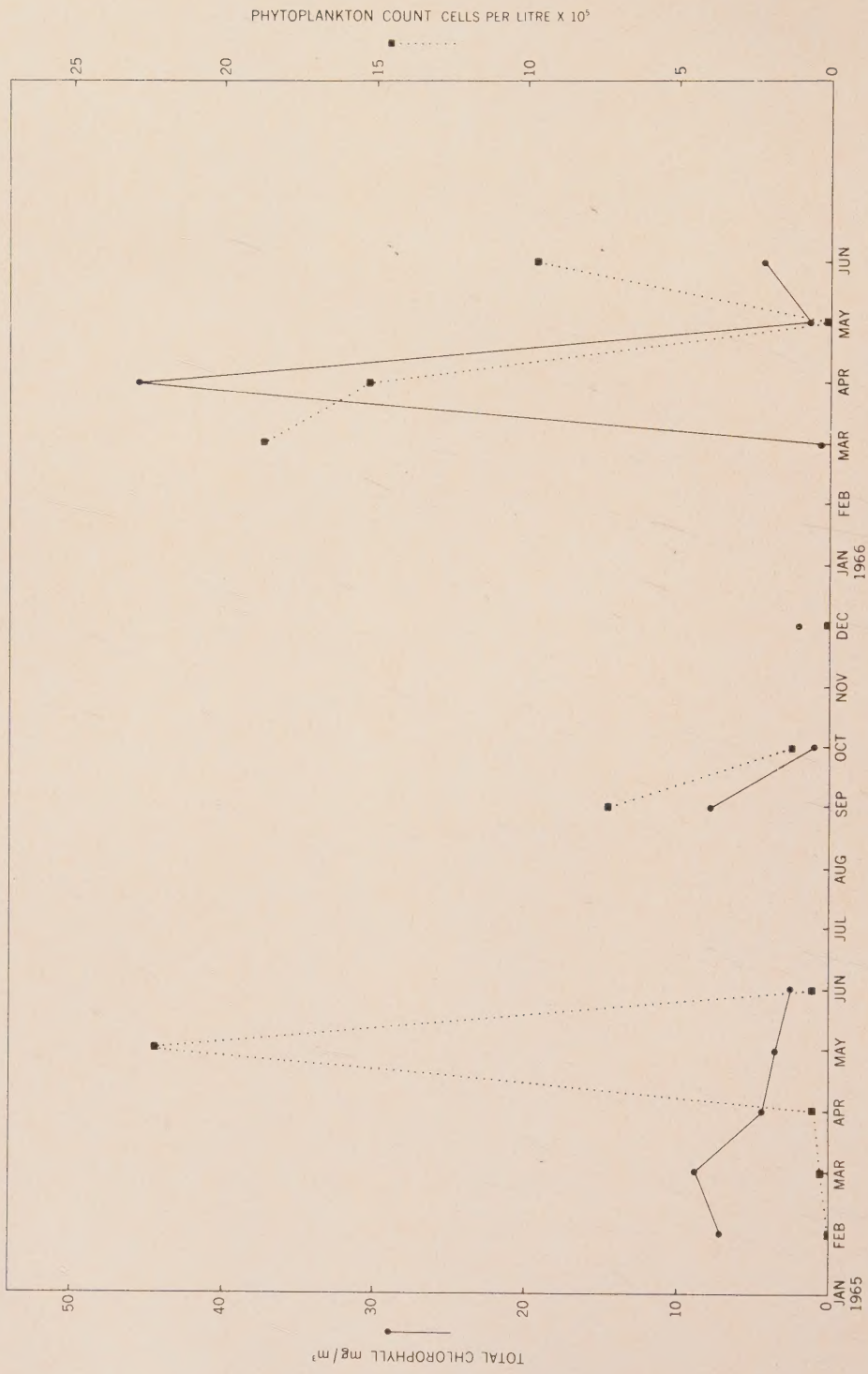

FIG. 2. CHLOROPHYLL CONTENT COMPARED WITH PHYTOPLANKTON CELLS AT STATION 24-1·5

Trigsurvey 1969.

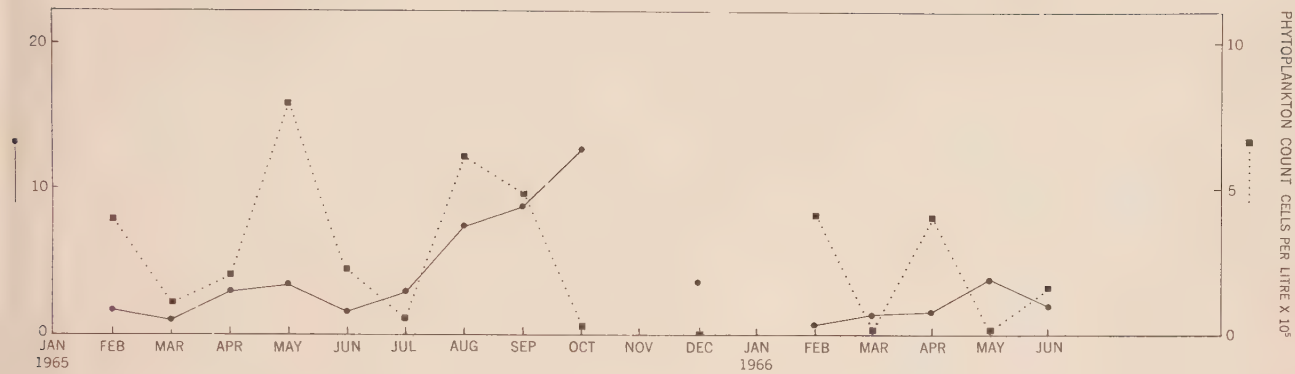

FIG. 3. CHLOROPHYLL CONTENT COMPARED WITH PHYTOPLANKTON CELLS AT STATION 52-1

Trigsurvey 1969.

TOTAL CHLOROPHYLL AND N50V SETTLED-VOLUMES

Regression equations were determined for the chlorophyll content and the settled-volumes of the N50V net samples for the months of February to June 1966. These equations showed no relationship between the two variables as can be seen graphically in Figure 4.

For each month, however, most of the deviations from the calculated relationship could be explained by reference to the overall size and the chromatophore size of the species concerned. Settled-volume is not a good parameter for comparison as the packing density of the cells varies according to the size and shape of the species concerned. No direct relationship between the total chlorophyll content and the settled-volume can be established without considering the actual species.

CHLOROPHYLL VARIATION

The variations of chlorophyll concentration in the inshore region are best shown graphically (Fig. 5). On the West Coast high chlorophyll values were recorded mainly in late summer and early autumn, where values up to 45 mg/m^3 were attained. The surface chlorophyll content was usually found to be higher than at 10m, but occasionally the 10m value exceeded that of the surface.

On the South Coast no clearly defineable pattern could be traced. In False Bay values higher than 7 mg/m^3 were recorded from July to October 1965 and a high value of 16 mg/m^3 was found in February 1966.

Offshore

The chlorophyll content 85 miles offshore was found to be less than 5 mg/m^3 with a few exceptions.

The West Coast values in excess of 5 mg/m^3 were recorded in late summer and autumn at Station 36-5, and on the South Coast chlorophyll peaks were sometimes recorded in winter and sometimes in summer.

TOTAL CHLOROPHYLL AND OXYGEN CONTENT RELATIONSHIP

The dissolved oxygen content corresponding to the chlorophyll recorded is given in Table I. From these results it appears that although oxygen and chlorophyll are related, this relation breaks down at times. It is evident that other oceanographic and biological factors would have to be considered before any definite correlation could be attempted.

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TABLE I. CHLOROPHYLL (CH) AND DISSOLVED OXYGEN (O_2) IN SEA-WATER SAMPLES, 1965-66

Year	Station	Depth m	January		February		March		April		May		June		July		August		September		October		November		December	
			Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L	Total ch mg/m³	O_2 ml/L
1965	80–1	0	—	5·32	0·67	5·17	1·14	5·06	2·42	5·01	1·31	5·24	2·23	5·41	3·77	6·23	2·00	5·53	1·80	6·19	2·33	5·70	—	—	0·64	5·51
		10	—	—	1·07	5·42	0·97	5·22	0·41	5·05	1·31	5·56	1·97	5·40	3·08	6·17	0·97	5·61	1·66	—	1·94	5·77	—	—	0·19	5·63
	72–1	0	0·79	5·34	0·87	5·23	1·07	5·17	0·45	5·13	1·91	5·29	2·90	5·64	6·17	5·97	1·32	5·67	2·09	5·91	5·46	6·03	—	—	1·04	5·61
		10	—	5·43	0·98	5·74	0·69	5·28	0·72	5·11	1·70	5·36	2·54	5·64	1·36	5·97	0·92	5·74	2·11	5·91	7·10	5·80	—	—	1·22	5·65
	60–1	0	1·13	5·37	0·55	5·67	4·17	5·45	6·82	5·85	2·25	5·38	3·93	6·17	3·03	6·02	—	—	3·01	6·20	5·08	6·03	—	—	3·96	5·19
		10	—	5·46	1·80	5·87	2·73	5·48	7·28	5·88	1·99	5·51	4·15	6·20	1·95	5·82	—	—	3·69	6·43	3·94	6·05	—	—	2·90	6·03
	52–1	0	3·70	5·92	2·55	5·56	1·73	5·50	0·99	5·92	3·34	5·56	1·83	5·66	8·58	7·10	9·86	6·23	9·58	6·15	9·70	6·83	—	—	2·39	5·31
		10	—	5·88	1·63	5·66	1·05	5·65	2·89	6·06	3·41	5·51	1·47	5·71	2·88	6·46	7·37	6·12	8·75	6·09	12·64	6·78	—	—	3·49	5·77
	44–1	0	9·96	7·46	0·48	4·14	19·84	6·34	2·29	6·43	4·40	—	3·23	5·19	1·68	5·69	7·31	6·35	—	5·78	4·75	6·73	—	—	9·26	6·80
		10	—	7·33	0·35	3·15	12·69	6·63	1·40	6·27	—	5·41	1·06	5·57	1·36	5·83	—	6·35	—	5·83	4·49	6·66	—	—	10·73	7·11
	36–1	0	2·17	6·77	12·08	8·44	11·11	8·27	2·26	6·07	1·91	5·97	3·61	6·02	5·72	6·12	3·38	5·91	4·89	7·42	7·19	6·75	—	—	1·56	6·18
		10	—	6·73	29·02	5·14	5·46	8·22	1·42	5·43	—	5·50	3·34	6·01	3·54	6·10	—	5·91	4·13	6·85	6·33	6·49	—	—	1·86	6·35
	24–1·5	0	—	6·13	1·61	6·29	26·37	6·57	7·35	5·90	5·51	7·67	2·90	6·33	1·21	6·41	2·45	6·38	4·37	7·18	0·60	3·51	—	—	2·51	5·28
		10	—	5·40	7·30	4·77	8·87	3·16	4·55	3·70	3·73	5·99	2·62	6·43	4·46	6·05	—	6·13	7·89	6·19	1·05	2·62	—	—	2·22	5·24
	80–5	0	0·65	5·13	0·38	5·12	—	5·27	1·01	5·05	1·26	5·46	1·74	5·32	5·90	5·83	1·74	5·59	1·46	5·93	2·00	5·75	—	—	2·12	5·65
	72–5	0	2·86	5·24	0·35	6·12	0·53	5·17	0·48	5·26	1·02	5·56	1·89	5·61	4·27	5·66	1·40	5·84	1·96	5·59	1·11	5·68	—	—	1·33	5·56
	60–5	0	0·36	5·19	0·00	5·17	0·53	5·40	0·23	4·87	1·21	5·38	1·34	5·37	1·04	5·72	1·73	5·70	1·11	5·51	1·44	5·73	—	—	1·12	5·44
	52–5	0	0·89	5·20	0·18	5·45	0·80	5·35	0·39	5·33	1·26	5·31	0·62	5·69	0·76	5·68	—	—	1·08	5·91	1·43	5·89	—	—	1·12	5·54
	44–5	0	1·47	5·52	0·19	5·29	1·23	5·23	0·67	5·44	1·15	5·54	0·56	5·54	3·03	5·85	1·11	5·62	—	5·88	1·24	5·15	—	—	0·87	5·26
	36–5	0	0·27	5·24	15·88	5·24	0·28	5·18	0·55	5·29	1·30	5·22	0·87	5·81	1·01	5·82	1·04	5·89	1·60	6·16	0·72	5·88	—	—	1·77	5·33
	24–5	0	1·09	5·78	0·46	5·32	1·89	5·40	0·76	5·70	1·06	5·49	1·10	5·77	1·22	6·35	1·00	5·75	1·31	5·82	0·69	5·86	—	—	1·52	5·61
1966	80–1	0	—	—	0·34	5·14	4·98	5·45	—	5·19	1·84	5·47	2·32	5·59												
		10	—	—	0·43	5·37	17·10	5·58	—	5·23	1·90	5·59	1·78	5·76												
	72–1	0	—	—	0·77	5·26	0·46	5·20	—	5·19	1·56	5·47	0·53	5·86												
		10	—	—	0·44	4·85	0·67	5·33	—	5·14	1·79	5·81	5·46	5·86												
	60–1	0	—	—	21·42	7·52	0·95	5·60	7·54	5·78	0·78	5·59	2·93	5·89												
		10	—	—	0·75	7·26	0·85	5·64	5·35	5·66	1·03	5·69	2·65	5·89												
	52–1	0	—	—	16·44	8·09	1·39	5·55	2·23	5·85	5·28	6·81	1·97	6·38												
		10	—	—	0·56	7·93	1·34	5·64	1·51	5·90	3·73	6·69	1·97	6·88												
	44–1	0	—	—	1·57	—	9·04	7·08	6·22	6·57	2·42	6·16	7·13	7·93												
		10	—	—	1·95	—	5·27	6·11	1·37	5·05	2·41	5·04	5·83	7·23												
	36–1	0	—	—	1·35	7·31	1·99	6·84	13·72	6·69	3·69	5·96	10·58	6·73												
		10	—	—	1·43	7·99	1·68	5·31	0·17	6·81	3·98	5·95	6·55	6·78												
	24–1·5	0	—	—	5·43	7·65	0·52	4·76	18·37	8·96	3·98	5·17	5·89	5·74												
		10	—	—	3·97	7·46	0·66	3·33	45·76	5·05	1·32	3·65	4·48	5·54												
	80–5	0	—	—	0·25	5·12	1·64	5·17	—	5·23	1·19	5·43	1·38	5·54												
	72–5	0	—	—	0·27	5·17	0·12	4·98	—	5·11	0·96	5·47	0·80	5·50												
	60·5	0	-	—	24·04	5·12	0·37	5·18	1·16	5·28	1·03	5·45	0·89	5·51												
	52–5	0	—	—	10·93	5·28	0·90	5·42	1·26	5·47	0·42	5·43	6·96	5·63												
	44–5	0	—	—	0·22	5·43	0·19	5·50	0·38	5·49	—	5·50	0·66	5·71												
	36–5	0	—	—	0·31	5·67	0·59	5·33	4·28	5·38	1·66	5·42	0·87	5·66												
	24–5	0	—	—	0·77	5·38	0·84	5·44	1·00	5·57	0·93	5·48	0·69	5·81												

TABLE II: CHLOROPHYLL (CH) IN N50V PLANKTON SAMPLES, 1966

1966	February		March		April		May		June	
Station	Total ch	Settled volume	Total ch	Settled volume	Total ch	Settled volume	Total ch	Settled volume	Total ch	Settled volume
	μg	ml	μg	ml	μg	ml	μg	ml	μg	m
80–1	—	—	36·31	1·0	14·22	0·1	20·30	1·1	0	0·2
80–3	—	—	44·27	2·0	7·39	0·2	0·69	0·6	10·11	0·3
80–5	—	—	—	—	6·11	0·4	5·81	1·2	5·71	0·4
76–1	—	—	9·02	1·0	—	—	10·76	2·0	352·63	14·0
76–3	—	—	13·63	0·2	—	—	6·01	0·8	22·74	0·5
72–1	—	—	29·81	0·5	45·38	1·0	18·52	1·0	289·95	8·4
72–3	—	—	—	—	2·26	0·2	1·97	0·6	9·67	0·7
72–5	—	—	—	—	7·13	0·1	3·73	0·4	4·65	0·3
68–1	—	—	16·95	1·0	23·75	0·5	290·29	20·0	249·20	9·6
68–3	—	—	—	—	2·68	0·3	3·22	0·4	—	—
64–1	—	—	29·30	0·5	30·08	4·3	19·51	2·0	—	—
64–3	—	—	—	—	8·61	0·2	4·40	0·8	—	—
60–1	—	—	49·08	2·0	14·38	1·4	8·35	1·1	189·41	8·9
60–3	—	—	5·95	0·5	1·52	0·3	3·60	0·8	—	—
60–5	—	—	1·93	0·2	2·93	0·3	1·73	0·7	3·11	0
56–1	—	—	63·73	0·2	34·41	3·4	50·37	2·5	117·71	0·2
56–3	—	—	—	—	28·86	0·8	4·23	0·5	12·84	0·6
52–1	—	—	—	—	47·14	2·0	104·23	2·3	66·73	1·9
52–3	—	—	5·83	0·1	35·44	0·8	10·97	2·0	3·30	0·3
52–5	—	—	—	—	10·77	0·6	1·55	0·4	1·12	0
48–1	—	—	—	—	20·91	0·8	232·68	10·2	164·15	3·9
48–3	—	—	4·20	1·0	—	—	9·48	1·5	63·02	1·3
44–1	—	—	26·95	0·5	25·53	0·7	7·84	2·0	73·32	1·1
44–3	—	—	3·18	1·0	66·04	2·2	34·92	1·8	2·35	0
44–5	—	—	—	—	7·20	0·5	12·01	1·0	1·32	0
40–1	217·33	10 (4)	53·07	2·0	274·84	20·0	18·49	2·6	90·79	1·2
40–3	1·16	0	3·36	0·5	46·80	0·9	—	—	1·68	0·4
36–1	37·14	8 (2)	—	—	439·01	7·6	11·52	4·0	311·67	4·8
36–3	3·07	8	8·39	0·5	66·47	1·5	—	—	2·67	0·3
36–5	3·22	10	2·85	0·5	9·77	0·1	6·95	0·8	0·80	0
32–1	43·68	16 (3)	63·87	2·0	16·53	1·6	9·89	2·5	296·66	11·1
32–3	1·40	2	0	0	20·39	0·3	6·96	0·7	1·13	0·2
28–1	—	—	44·47	1·5	—	—	6·96	1·3	19·33	1·0
28–3	—	—	—	—	—	—	4·89	0·4	6·91	0·3
24–1·5	63·15	26 (5)	—	—	—	—	2·16	2·7	643·72	22·0
24–3	21·32	8	—	—	34·45	1·0	1·01	1·1	19·71	0·7
24–5	2·76	6 (1)	13·90	3·0	—	—	0·51	1·0	4·54	0·3
20–1	10·05	32 (12)	—	—	10·25	0·9	4·28	2·5	2·40	1·1
20–3	—	—	—	—	31·01	1·0	3·03	0·9	3·46	0·4
				*	*	*	*	*	*	*

* After filtering sample through N70 netting.

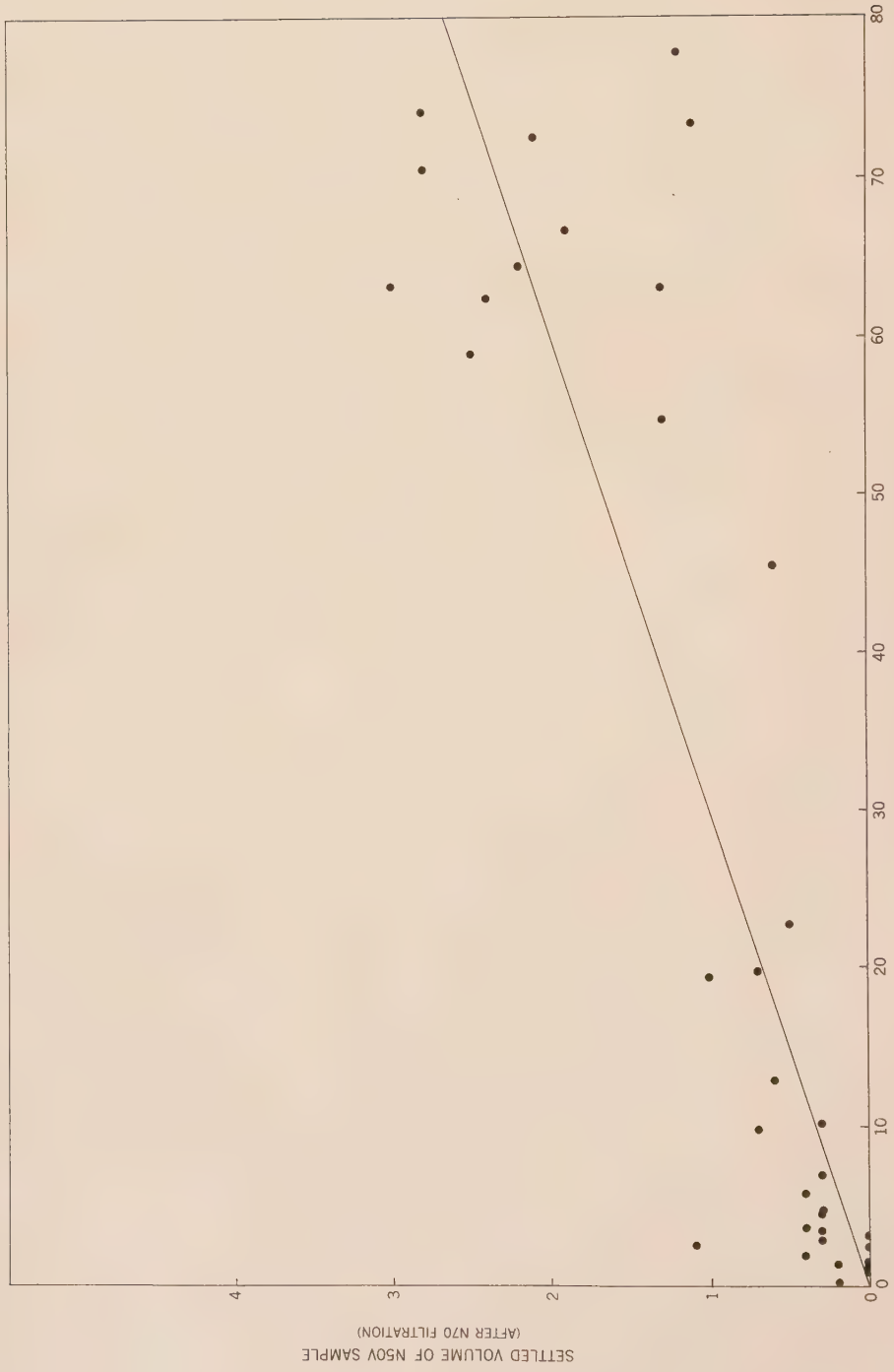

FIG. 4. RELATIONSHIP BETWEEN CHLOROPHYLL AND SETTLED VOLUME – JUNE 1966

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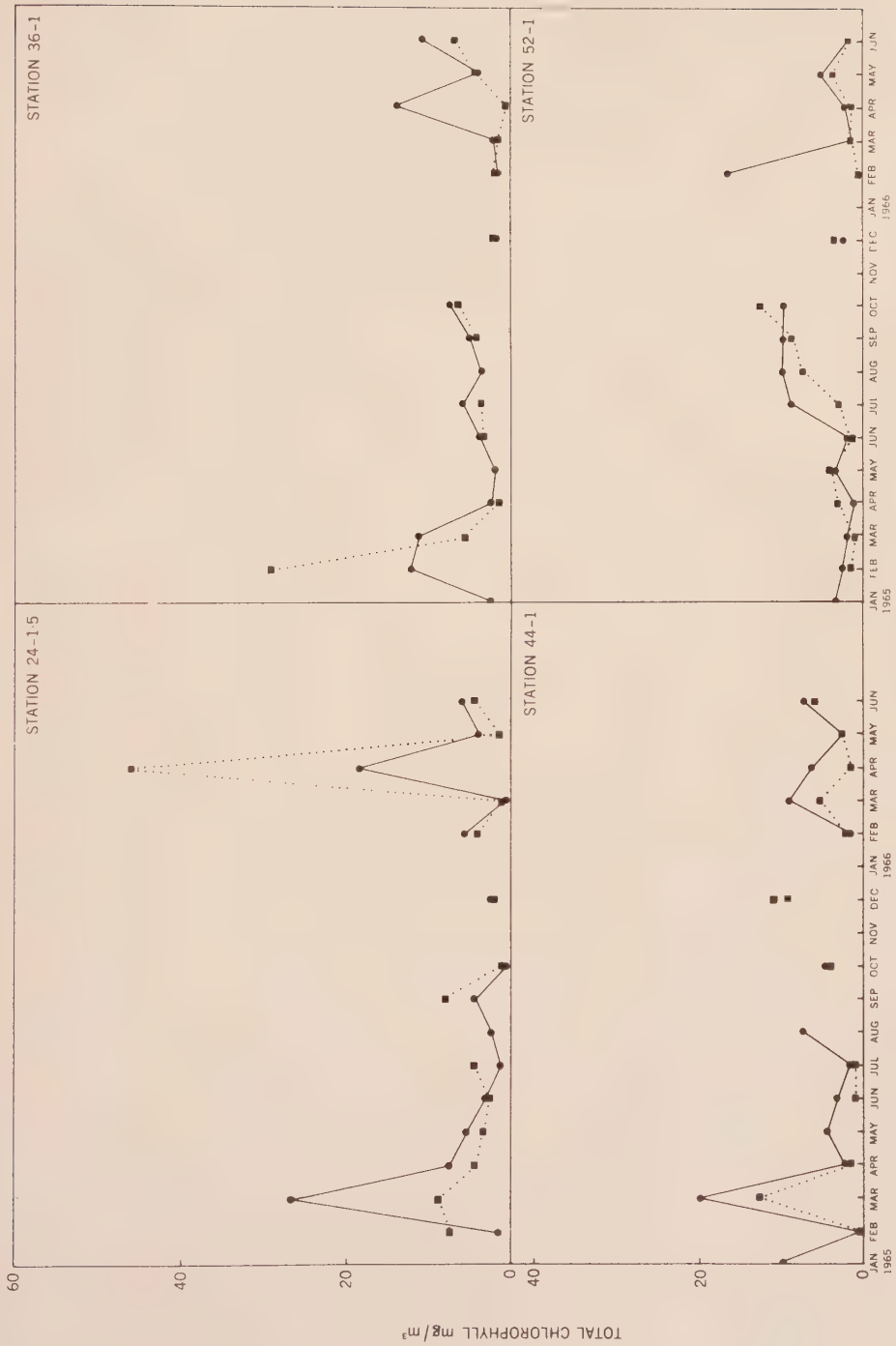

FIG. 5. MONTHLY VARIATION IN CHLOROPHYLL CONTENT

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THE OXYGEN - MINIMUM LAYER BETWEEN THE SURFACE AND 1000 m IN THE NORTH-EASTERN SOUTH ATLANTIC

G.A. VISSER

The waters of the north-eastern South Atlantic contain less oxygen between about 50 m and 1000 m than at either lesser or greater depths. This is the most marked feature of the water in the region presently under discussion.

Several investigators have discussed this phenomenon which occurs in most of the major oceans. One group seems to favour an explanation in terms of dynamics for the existence of such a layer while another group apparently prefers the bilogical approach to the problem. The former concept relates the oxygen-minimum layer purely to dynamically controlled circulatory processes. The biochemical approach, held mainly by Seiwell (1937, 1938), suggests that this layer is controlled biochemically. More recently, various authors seem to agree that the most overwhelming factor controlling the oxygen-minimum layer is the oxidation of organic matter derived primarily from the surface layers of the ocean.

An interesting feature of this layer is the fact that it is accompanied by maxima in the amounts of available phosphate, nitrate, and silica. However, no detailed analysis of this phenomenon has been made in the case of the latter two components. The most detailed mapping of the oxygen and phosphate contents in the oxygen-minimum layer of the north-eastern South Atlantic was done by Wattenberg (1938, 1939). The positions of the series of stations occupied during the complete investigation of the *Meteor* from 1925-1927, is presented in Figure 1.

EXTENT AND MAGNITUDE OF THE OXYGEN-MINIMUM LAYER

The 3.0 ml/l isopleth was arbitrarily chosen as the boundary of the oxygen-minimum layer. Horizontally this layer stretches from the west coast of Africa, between 24° S and the equator, to about 35° W, between 15° S and 5° S (Fig. 2). South of 24° S it extends southwards along the coast of South-West Africa, close to the Continental Slope and the Continental Shelf (Stander 1964) – the "Deep Compensation Current" (Fig. 3). Along the west coast of Africa the oxygen-poor layer is found between *circa* 50 m and *circa* 900 m. Towards the west the vertical extent of this layer decreases and is found between about 350 m and 450 m (Fig. 4).

The lowest oxygen values (less than 0.5 ml/l) were found close to the west coast of Africa. This oxygen-deficient core of the water is situated at a depth of about 350 m (Fig. 4). Towards the west the magnitude of the oxygen content increases slowly to about 3 ml/l due to lateral mixing and an apparent slow-down in the oxidation processes (Fig. 5).

From Figure 2 it is clear that the oxygen-minimum layer of the north-eastern South Atlantic is continuous with an almost similar layer in the south-eastern North Atlantic. These two extensions seem to be separated by a tongue of relatively higher oxygen which covers the region around the equator.

BIOLOGICAL, CHEMICAL AND PHYSICAL FACTORS WHICH INFLUENCE THE OXYGEN-MINIMUM LAYER

The oxygen-minimum layer in the north-eastern South Atlantic is associated with the region of active upwelling along the west coast of Africa. The upwelling of nutrient-rich water from intermediate depths creates the ideal environment for a large planktonic population. Hart and Currie (1960) presented a detailed mapping of the microplankton populations in the area just south of the principal origin of the oxygen-deficient layer (Figs. 6, 7 and 8). They give a summary of the findings concerning the zooplankton populations. It is apparent that most of the species were found at depths ranging from 50 m to about 500 m. Figure 9 also shows the planktonic population density as found by the investigators of the *Meteor* data.

Many authors (e.g. Hart and Currie 1960) emphasise that the phytoplankton population is dominated by diatoms. In several cases the latter were taken as an index of the distribution of phytoplankton. From all these distribution maps it is clear that the region of upwelling is characterized by an exceptional abundance of plankton in the shallower layers, primarily in the euphotic zone. The phytoplankton provides the necessary food supply for the zooplankton which in turn serves as a food supply for an abundance of fish.

Nielsen (1937) also stressed that the maximum number of zooplankton occurs some time after the phytoplankton population has reached a peak in abundance. This is probably due to the fact that the phytoplankton must first create an environment which is rich in food for maximum development in the zooplankton population. A further delay in the occurrence of maximum numbers of zooplankton is

caused simply because the development of the latter is usually slower than that of the phytoplankton.

Moberg (1928) pointed out that the oxygen-minimum layer coincides with a maximum distribution of phytoplankton in the region of active upwelling along the coast of South California. This phenomenon was also mentioned by Wattenberg (1938) in his investigation of the *Meteor* data. These authors agree that the rich planktonic environment supplies the large amount of oxidizable organic matter (Wattenberg: olivgrüne Zellen) which is important in the creation of an oxygen-poor layer (Fig. 10). The organic matter consists of large numbers of dead plankton and planktonic excretions. Oxidation of this material is responsible for the consumption of a considerable amount of oxygen.

The amount of oxygen consumed during the oxidation process depends basically on the speed of the oxidation reactions. Rakestraw (1947) found that the oxidation is at a maximum during the first number of days of the reaction period. After about 50 days the oxidation process decreases to negligible proportions. Zobell (1940) further showed that the oxidation of the organic matter is not hampered by the decrease in oxygen content of the water while the process is at work. He found that the oxygen tension (in the range 0.31 to 12.74 ml/l) had a negligible effect on the rate of oxidation of organic matter in the sea. Therefore, it is quite obvious that the low oxygen content in the core of the oxygen-minimum layer of the north-eastern South Atlantic will in no way retard the oxidation processes. Rakestraw's findings might serve in part, as an explanation for the decrease in oxygen depletion of the oxygen-poor layer towards the west.

Further depletion of the oxygen content occurs as a result of the respiratory processes of all the planktonic organisms. These processes will certainly play an important role in oxygen consumption because of the large numbers in which the phytoplankton and zooplankton are present in the area under consideration in this report.

Decomposition, both bacterial and chemical, of bottom sediments which are rich in organic matter apparently also serves to increase the intensity of the oxygen deficiency where the specific layer originates along the coast of Africa. It was established that the bottom sediments in this region are rich in organic matter of planktonic origin. This phenomenon can best be recognized in the southward protrusion of the oxygen-minimum layer along the coast of South West Africa (Fig. 3).

The settling velocity of particulate organic matter and planktonic detritus seems to play an important role in the depth distribution of the oxygen-minimum layer. It should also be borne in mind that the settling velocity depends, to a large extent, on the vertical density gradient of the water and the sizes of the individual detrital particles. The preceding factors may account for the gradual deepening of the core of the minimum layer in the initial stages of its formation (Fig. 4), and also for the relatively large vertical extent of the whole layer because the larger particles will sink rapidly while the smaller ones will sink rather slowly. Furthermore, the particles will attain a lesser sinking velocity as they go deeper, because of the increase in the vertical density gradient and the decrease in size of individual particles due to decomposition.

The effect of temperature is very important in the bacterial oxidation of organic material and planktonic detritus. Wattenberg (1938) presented a plausible picture (Fig. 11) of the temperature effect on the decomposition and also of the oxygen consumption due to the presence of a maximum amount of organic matter (olivgrüne Zellen). The combined effect clearly gives an explanation for the region of maximum oxygen consumption in the core of this particular layer. Figure 11 was constructed from observed average conditions at *Meteor* station 143 (Fig. 1) as a representative example of the region under consideration.

Renewal of oxygen due to biological activities occurs mainly as a result of the photosynthetic processes of the phytoplankton. These processes apparently dominate the respiratory processes in the surface layers. However, in the thermocline layer where active organic decomposition is taking place, the consumption of oxygen seems to be the predominating effect. Richards (1957) stressed this phenomenon when he stated that the photosynthetic production of oxygen exceeds respiratory consumption down to the "compensation depth". Below the "compensation depth" photosynthetic production continues, but other processes cause a net loss in oxygen content. In regions of intense photosynthetic activity, such as the area of active upwelling along the west coast of Africa, the compensation depth is shallow due to the decrease in the transparency of the water.

Another important feature of the oxygen-minimum layer in the north-eastern South Atlantic is that it occurs within the thermocline where the rapid decrease in temperature causes a sharp increase in density, which in turn results in the formation of a very stable layer between *circa* 50 m and *circa* 700 m (Fig. 10). The layer between the sea surface and about 50 m, "the mixed layer", is well aerated because of relatively rapid vertical mixing. The oxygen which is consumed by the respiratory and

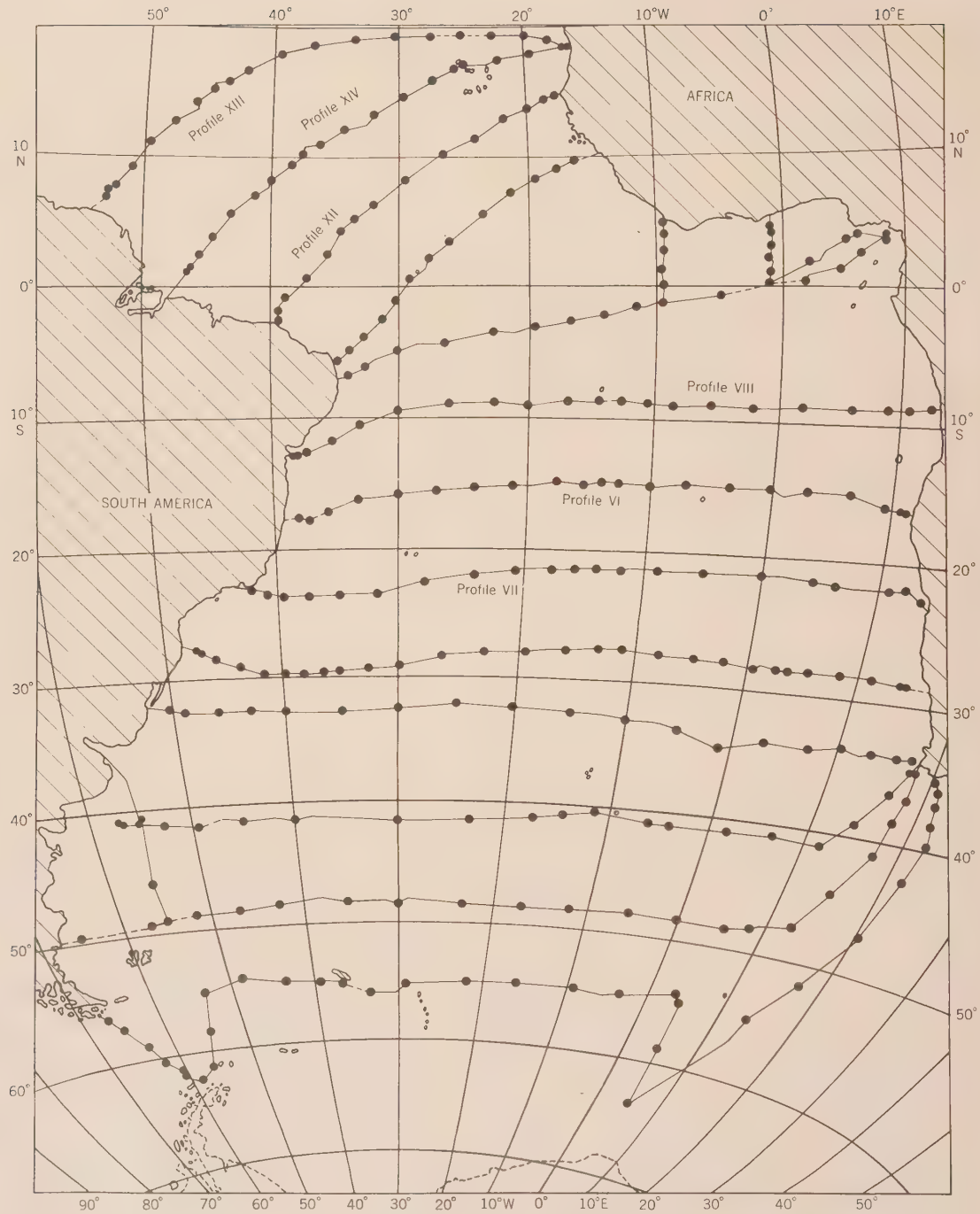

FIG. 1 . POSITION OF STATIONS OCCUPIED BY THE METEOR, 1925/1927 (REDRAWN FROM WATTENBERG 1938)

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oxidation processes in this layer, resulting in non-equilibrium oxygen concentrations, is rapidly replenished by photosynthetic processes and oxygen from the air at the sea surface.

The layer immediately below the thermocline is also fairly rich in oxygen because, by the time the sinking organic matter reaches the depths in which this layer is found, most of the active oxidation has apparently been completed. This layer also originates at the sea surface in the high southern latitudes where the surface waters are exceptionally rich in oxygen.

The thermocline layer, on the other hand, is much less subject to vertical mixing because of its great stability. The only type of mixing that does occur is lateral mixing along surfaces of constant potential density (Montgomery 1938; Redfield 1942). This lack of vertical mixing may also serve to intensify the oxygen deficiencies in this particular layer. Wattenberg (1938) clearly showed that the stability of the water masses in the South Atlantic Ocean and their oxygen content is closely related. In layers which are fairly unstable the oxygen-minimum layer disappears completely, while the most marked oxygen minima occur within the stable layers.

Some investigators also suggested that the rapid increase in density in the thermocline layer might cause a slow-down in the settling velocity of the planktonic detritus and other particulate organic matter (Seiwell and Seiwell 1938). This will then explain the region of maximum oxidation which coincides with the oxygen-minimum layer. However, this hypothesis was received with much skepticism by other investigators.

Wüst (1935) and other investigators emphasized their theory that the oxygen-minimum layer is closely related to ciculatory processes. They considered the minimum layer to be a slow-moving (or even stagnant) "boundary layer" between water masses. According to this theory the region between water masses moving in opposite directions becomes almost stagnant and causes a deficiency in the renewal of the oxygen that was consumed during bio-chemical and biological processes. In the north-eastern South Atlantic this theory is certainly not applicable because all the water masses (South Atlantic Central Water and Antarctic Intermediate Water) flow in the same direction. The only feature which seems to aid the formation of the oxygen-minimum layer is the low velocity at which the Benguela Current and its surrounding waters flow. The current velocities in this area do not usually exceed one knot. This gives the oxidation reactions the necessary time for the creation of an oxygen-poor layer close to the coast of Africa.

Taft (1963) briefly discussed the region in which the oxygen-deficient layer occurs. His findings, based on the characteristics of the 100 cl/t potential specific-volume surface, led him to suggest that the flow in this region might form a closed circulation (Fig. 12). If this is true then the renewal of oxygen will be seriously hampered, because the inflow of oxygen-rich water from the south will be limited. This may also cause an intensification of the minimum layer.

Other significant features of the oxygen-minimum layer are the well-defined maxima in phosphate, nitrate, and silica which occur in the vicinity of the core of this layer (Figs. 13 and 14). These maxima, however, are found at levels which are somewhat deeper than the core of the oxygen-minimum layer. Some investigators explain this phenomenon by suggesting that the oxidation reactions are actually a step-by-step process with the maximum release of the different chemical components occurring at different intervals during the oxidation process. Others suggested that the positions of the maxima might be related to the migrations of certain sections of the planktonic populations during which time some process may cause the maximal release of one of the chemical components while the organisms are at a particular depth. We could not find any conclusive evidence for either one of the two hypotheses. However, Richards (1957) did state that the phosphate and nitrate maxima are purely biochemical in origin, and that their concentrations are closely related to the amount of organic, oxygen-consuming material originally present.

CONCLUSION

The two processes by which the oxygen-minimum layer is controlled were mentioned in the introduction of this report. From the discussions in the preceding paragraphs it is obvious that an ideal environment for the formation of this oxygen-minimum zone (an abundance of both plankton and organic matter as a result of the active upwelling in this region) exists in the north-eastern South Atlantic.

As far as it concerns this particular layer it appears that the most important factors in its creation are the biochemical processes. The phenomenon, however, is not completely controlled by these processes. It is very clear that the intensity of this layer is aided to a large extent by physical factors such as the stability of the thermocline layer (density distribution) and a possible closed circulation. The former factor prevents vertical mixing, which might have eroded the oxygen-minimum layer tremendously. Therefore, it seems that physical processes do not control this layer either, but serve rather as complementary aids to the previously mentioned biochemical processes.

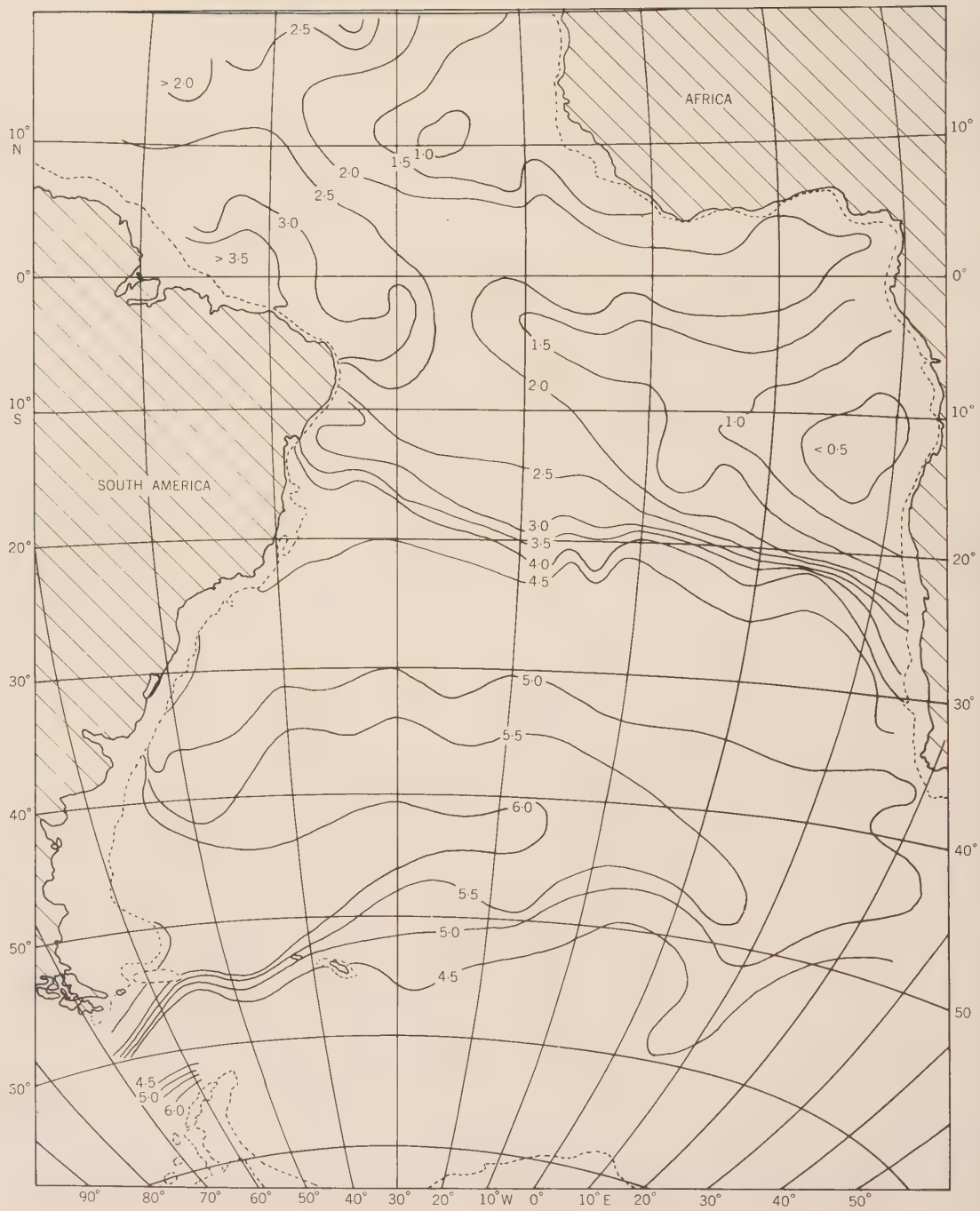

FIG. 2. DISSOLVED OXYGEN (ml/l) AT 400 m DEPTH (REDRAWN FROM WATTENBERG 1939)

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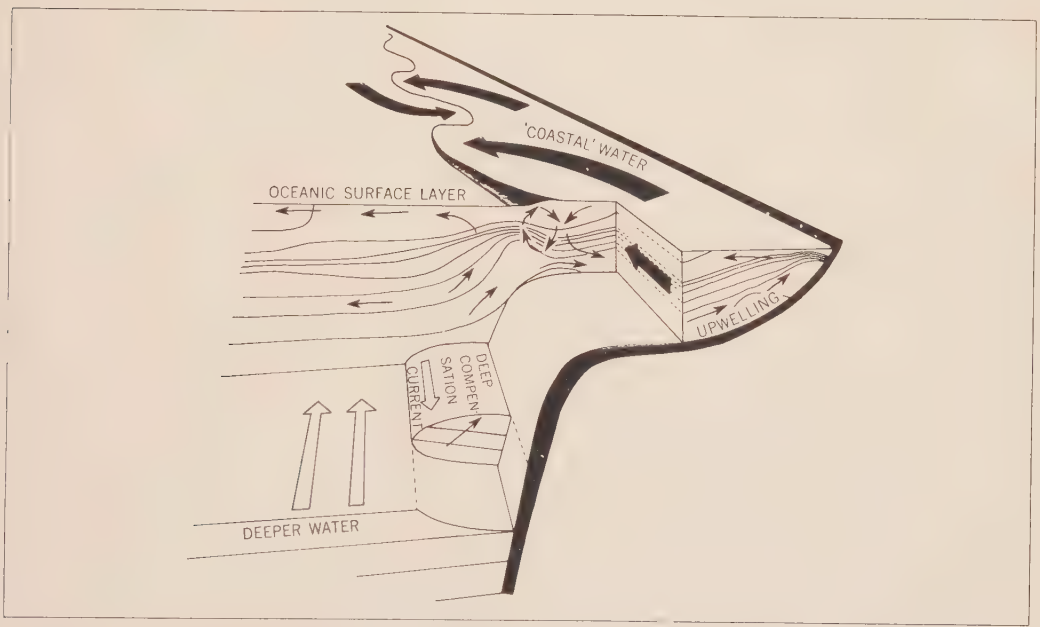

FIG. 3. UPWELLING AND PRINCIPAL WATER MOVEMENTS ALONG THE WEST COAST OF SOUTHERN AFRICA (REDRAWN FROM HART AND CURRIE 1960)

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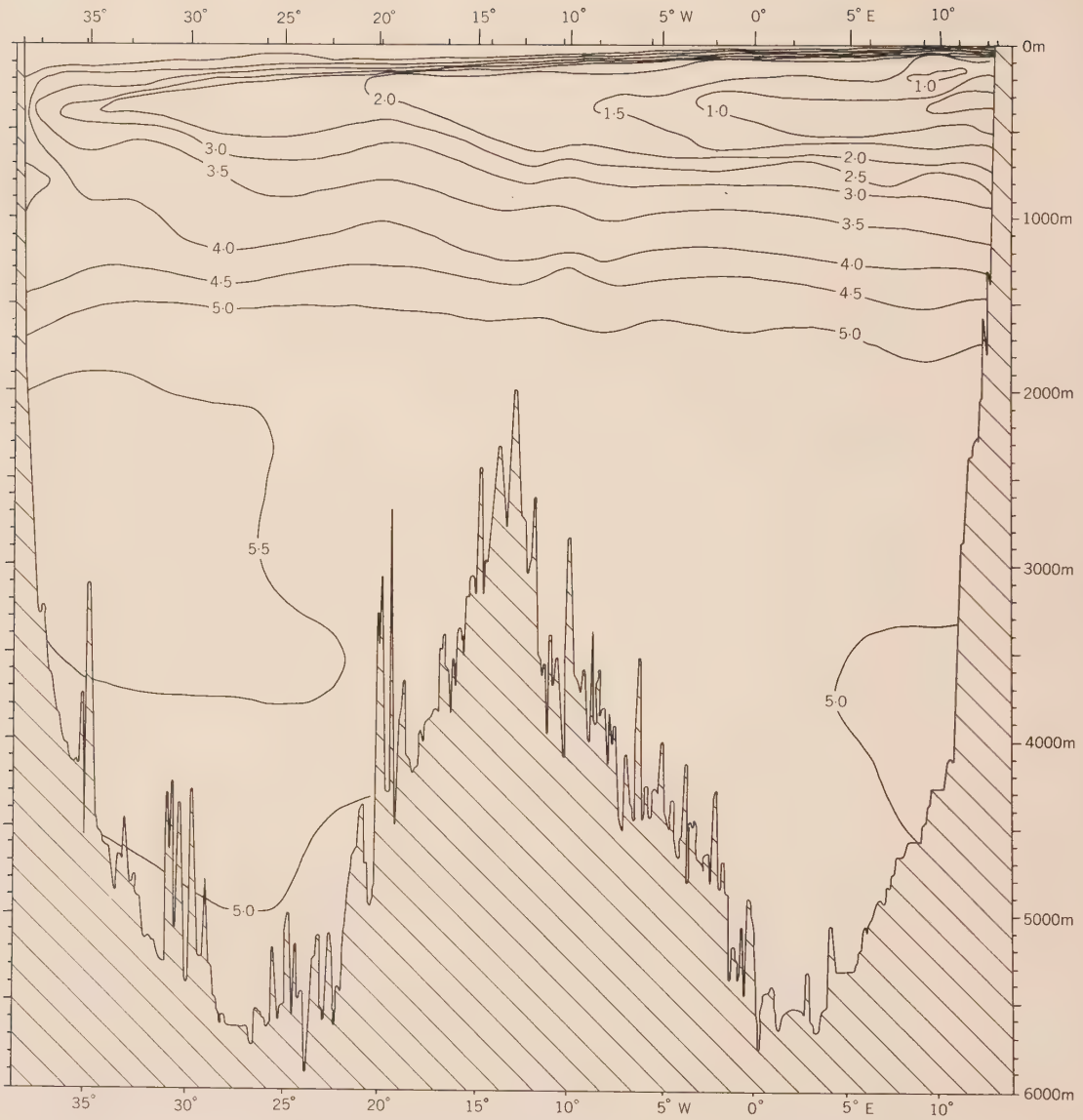

FIG. 4. VERTICAL DISTRIBUTION OF DISSOLVED OXYGEN IN N.E. SOUTH ATLANTIC-PROFILE VIII (REDRAWN FROM WATTENBERG 1939)

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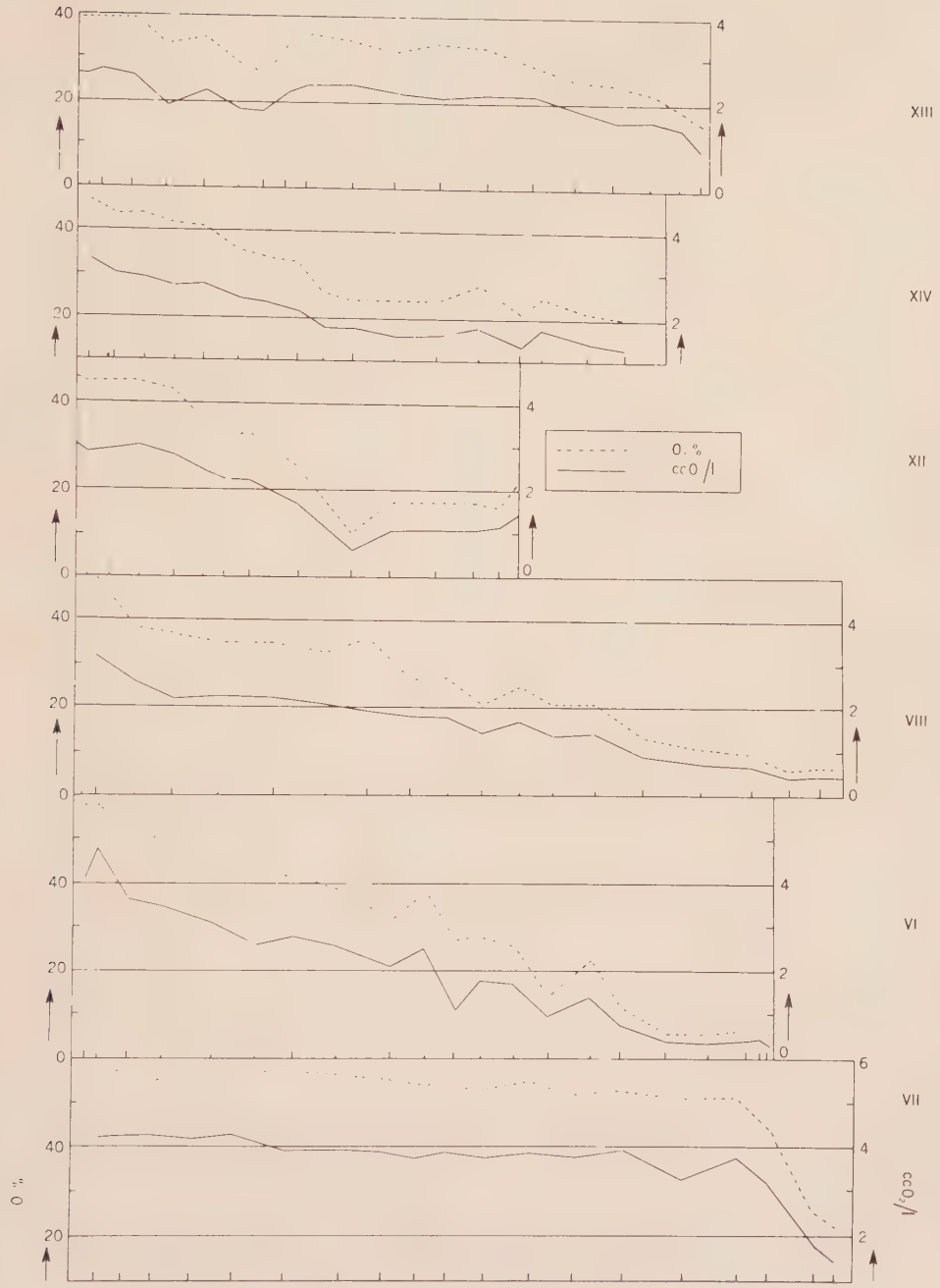

FIG. 5. WEST-EAST DISTRIBUTION OF DISSOLVED OXYGEN IN THE OXYGEN-MINIMUM LAYER OF THE SOUTH ATLANTIC-PROFILE VI-XIV (REDRAWN FROM WATTENBERG 1939)

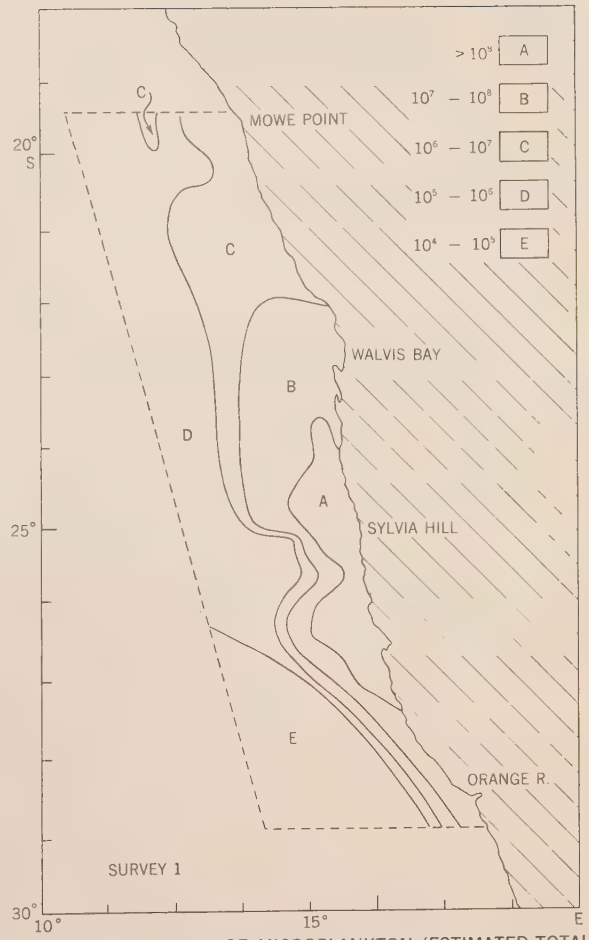

FIG. 6. DISTRIBUTION OF MICROPLANKTON (ESTIMATED TOTALS PER NET HAUL) – MARCH 1950 (REDRAWN FROM HART AND CURRIE 1960)

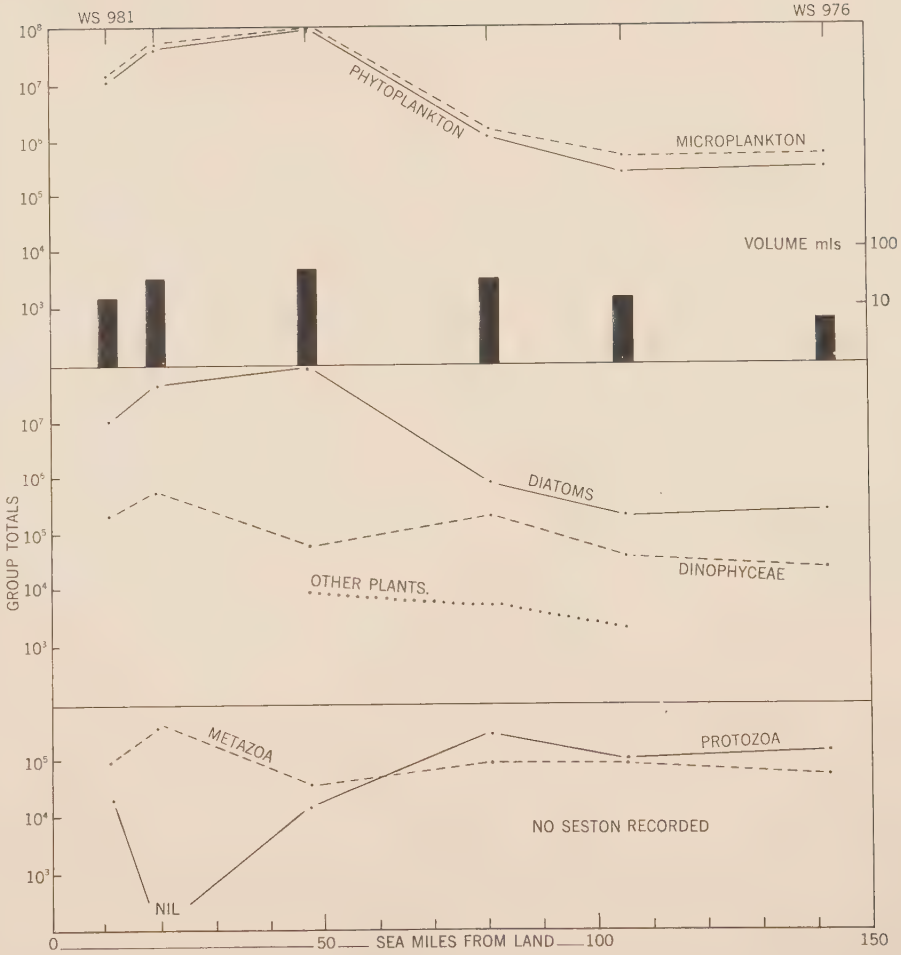

FIG. 7. DISTRIBUTION OF CHIEF MICROPLANKTON (ESTIMATED TOTALS PER NET HAUL) WALVIS BAY LINE, MARCH 1950 (REDRAWN FROM HART AND CURRIE 1960)

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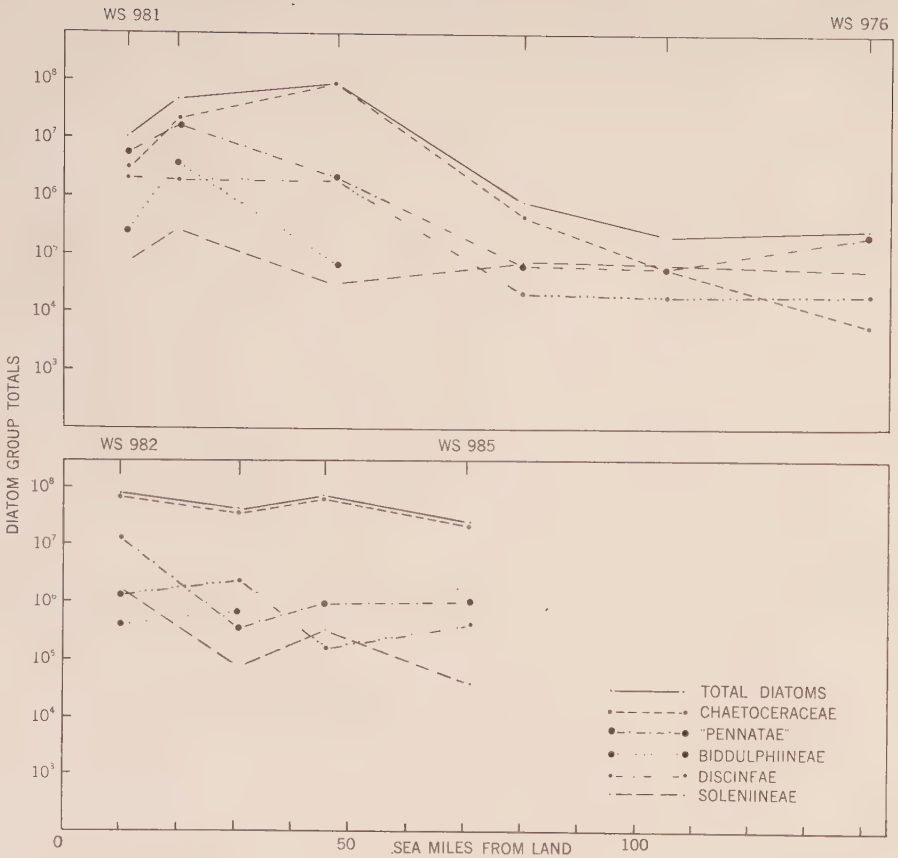

FIG. 8. ESTIMATED TOTAL DIATOMS AND CERTAIN DIATOM GROUPS FOR TWO LINES - (REDRAWN FROM HART AND CURRIE 1960)

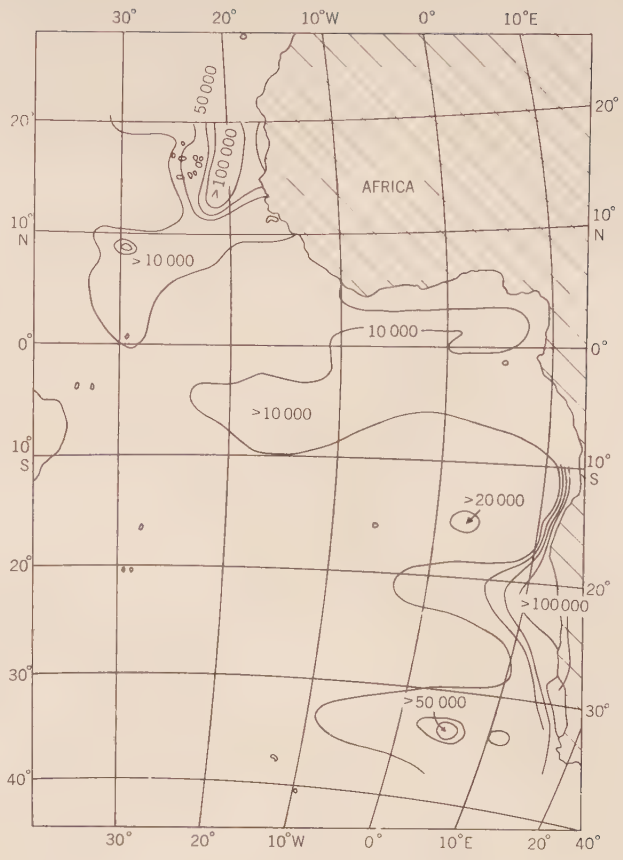

FIG. 9. ABUNDANCE OF PLANKTON (INDIVIDUALS PER LITER) IN THE 0-50 m LAYER (REDRAWN FROM WATTENBERG 1938)

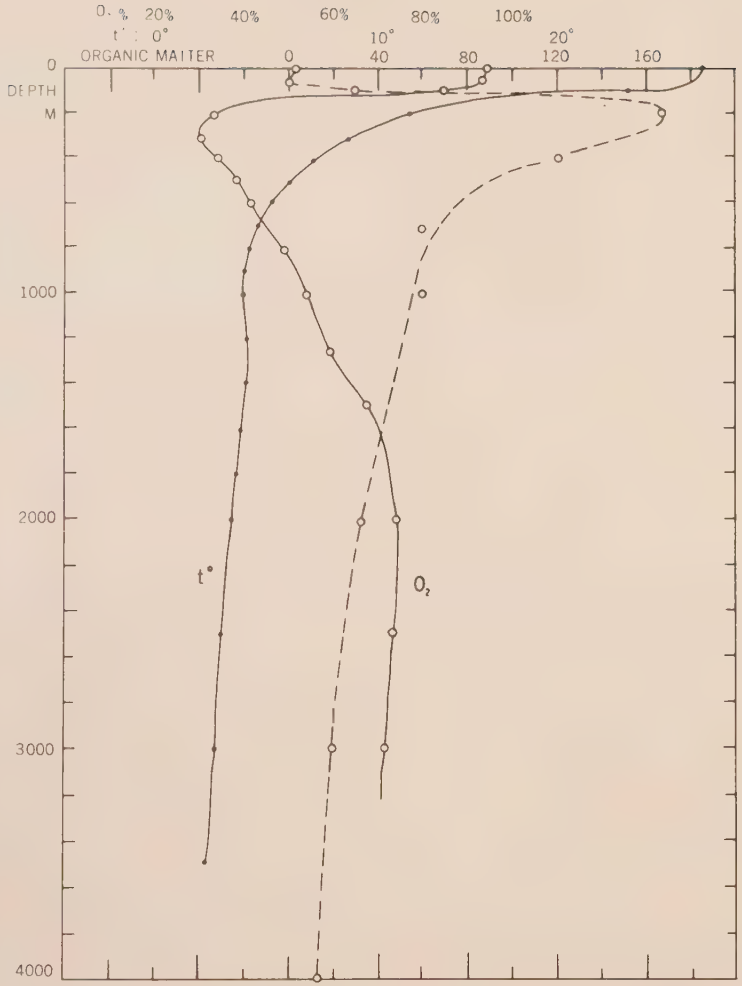

FIG. 10. VERTICAL DISTRIBUTION OF OXYGEN, TEMPERATURE AND ORGANIC MATTER IN THE EASTERN SOUTH ATLANTIC (REDRAWN FROM WATTENBERG 1938)

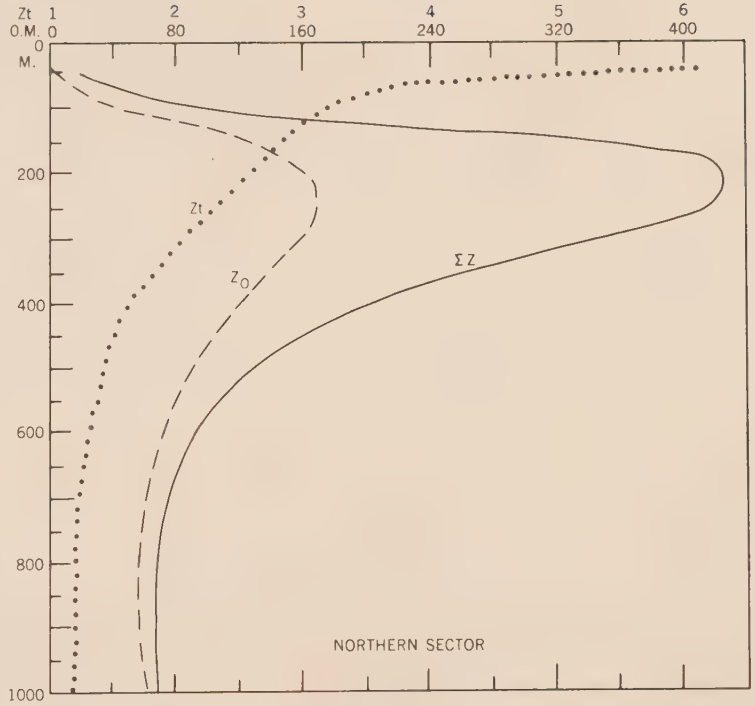

FIG. 11. VERTICAL OXYGEN CONSUMPTION FOR THE SOUTH ATLANTIC (LOWER LATITUDES): - Z_t CONSUMPTION DUE TO TEMPERATURE (METEOR STATION 143); - Z_0 CONSUMPTION DUE TO ORGANIC MATTER (OLIVGRÜNE ZELLEN); - ΣZ TOTAL CONSUMPTION (AFTER WATTENBERG 1938)

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FIG. 12. DISTRIBUTION OF DISSOLVED OXYGEN (ml/l) ON THE 100 cl/t POTENTIAL SPECIFIC VOLUME ANOMALY SURFACE (AFTER TAFT 1963)

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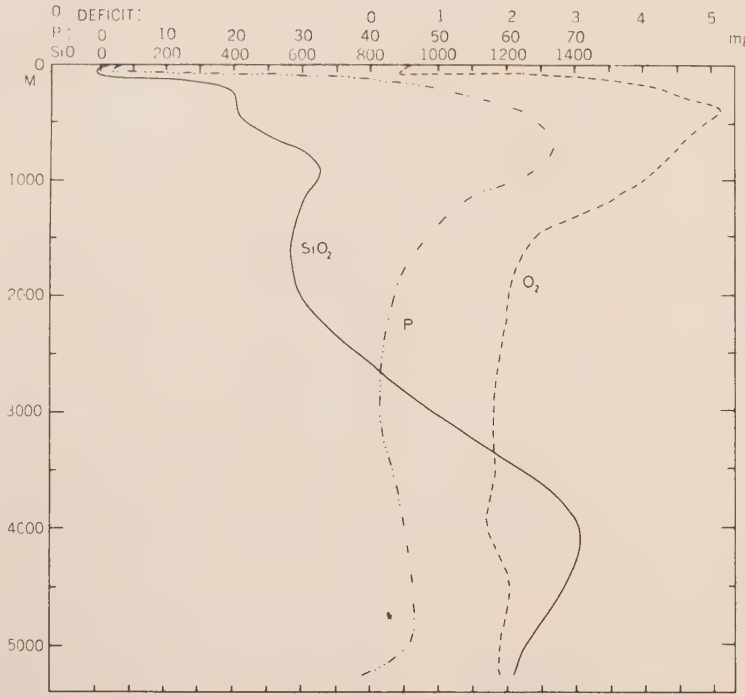

FIG. 13. VERTICAL DISTRIBUTION OF OXYGEN DEFICIT PHOSPHATE AND SILICATE IN THE UPWELLING WATER OFF THE WEST COAST OF AFRICA (AFTER WATTENBERG 1938)

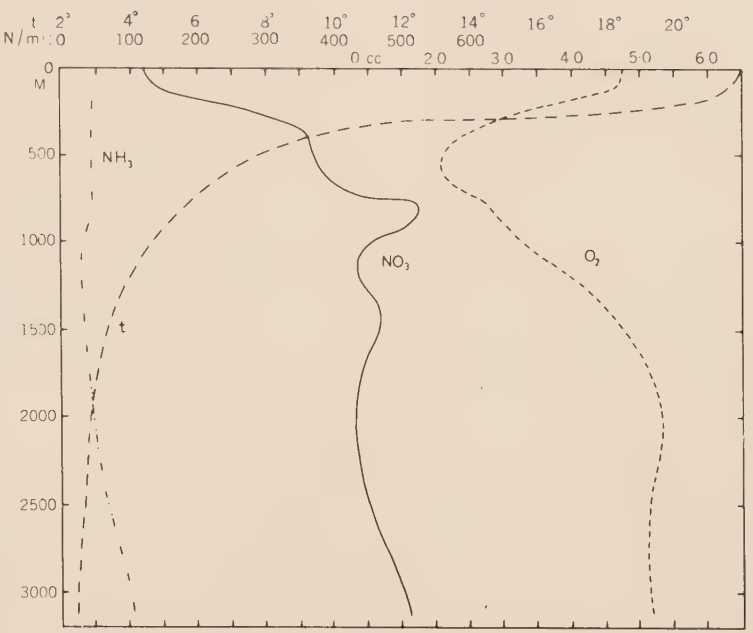

FIG. 14. VERTICAL DISTRIBUTION OF OXYGEN, NITRATE, AMMONIA AND TEMPERATURE AT A TYPICAL STATION (AFTER WATTENBERG 1938)

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AN IMPROVED APPARATUS FOR DETERMINING PLANKTON VOLUME

A.A. ROBERTSON

A rapid and accurate method for measuring the displacement volume of plankton was published by Yashnov in 1959. As the original paper was written in Russian, it is felt that a detailed description of the method, along with modifications made by us to the original apparatus might be of use to other workers.

After a number of trials with an apparatus (volume-meter) as described by Yashnov, it was decided to improve the construction to make it more durable, easier to handle and more error-proof under both laboratory and field conditions. The modified instrument was built at the Divisions' workshop and proved to be most suitable for measuring the diplacement volume of a large number of samples with the minimum chances of error, damage and contamination.

The instrument consists of three main components (Fig. 1), namely,

(i) Perspex cylinder,
(ii) Removable lower sealing cap, and
(iii) Removable brass cap.

The specifications (Fig. 2) are as follows: The cylinder (D) is made from perspex tubing with an outside diameter of 40 mm, and walls 4 mm in thickness. It is 88 mm long and has a volume of approximately 70 ml. The upper and lower edges are machined perfectly flat to take the two caps. At the lower portion of the cylinder, the outer diameter (8 mm from the bottom is reduced by approximately 2 mm on a lathe. Over this shoulder, a piece of fine-meshed nylon netting (G) is pulled taut and held in position by gluing the collar (F) over the shoulder. The outer surface of the collar is then machined flush with the rest of the cylinder. A few millimetres above the collar, a thin groove is turned into the cylinder to hold the rubber sealing ring (E) in position.

The removable sealing cap (H), which is made of a resin bonded fibre, is machined to fit tightly over both the collar and the rubber sealing ring.

The removable top cap (C) is made of brass and through its centre is threaded a brass rod (A) tapered to a fine point. The rod can be locked in position by means of the locking screw (B). An acentrically-placed hole, 8 mm in diameter, is drilled through the top surface of the cap to allow the tip of a burette to enter the cylinder. The cap should not fit too tightly over the top of the cylinder, but should rather be a smooth slip-fit.

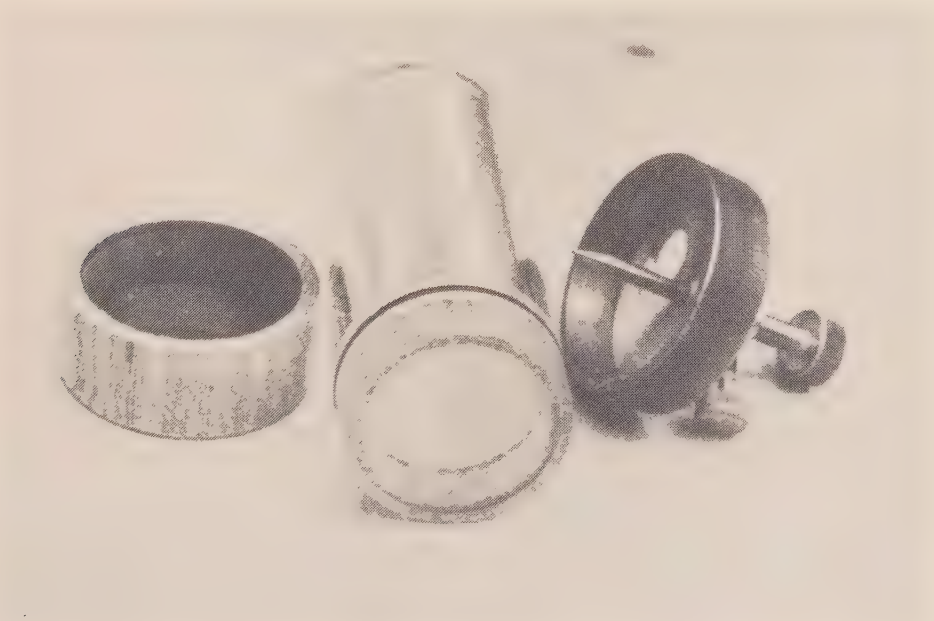

Fig. 1: Volume-meter showing three main components.

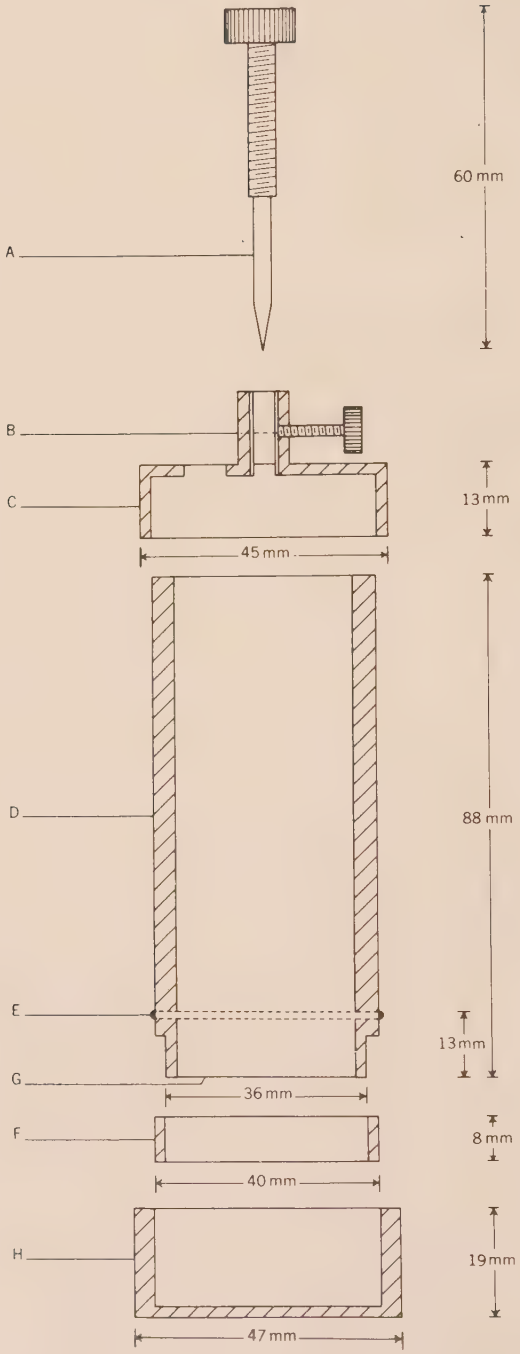

FIG. 2. DETAILS OF CONSTRUCTION OF VOLUME METER

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CALIBRATION AND VOLUME DETERMINATION

Before calibration, the complete instrument is washed thoroughly in a soap solution to remove any trace of grease or oil. The bottom sealing cap is dried but a thin film of water is left in the inside bottom edge. This will give a perfect seal and tests have shown that the variation in the amount of water left behind each time is negligible and far less than 0.1 ml. The cap is then pressed firmly into place and the top also positioned (Fig. 3).

Exactly 50 ml of titrant is then allowed to run from a burette into the cylinder through the off-centre hole in the cap. It is advisable to hold the instrument at a slight angle so that the jet of liquid strikes the wall of the cylinder. This helps to prevent the formation of air bubbles on the sides of the walls or under the gauze. Any bubbles formed can easily be removed by tapping the instrument lightly. After exactly 50 ml have been run off into the cylinder, the tapered brass rod is screwed down until the tip just touches the surface of the liquid. Care should be taken to ensure that the meniscus is properly formed. A slight rotational movement will solve this problem. Once the rod is in position the locking screw is tightened. The fluid is then drained off by removing the bottom cap.

The instrument, without bottom and top caps, is then clamped into a retort stand, and the sample to be measured is poured in. The walls of the cylinder are washed down with 5% neutral formalin (made up with filtered sea-water) and after they have been dried with a piece of filter paper, the sample is allowed to "drip" dry for a short period. This period will of course vary with different size samples. The bottom gauze is then dabbed gently a few times on a soft towel or piece of filter paper to absorb excess interstitial fluid. A "standard" stage of dryness should be determined. For normal size crustacean samples, this can be relatively simple. After daubing the guaze, most of the remaining interstitial fluid can be removed by placing one's mouth inside the top of the cylinder and blowing very gently. The pressure thus created, forces out the excess fluid and the gauze is once again gently daubed. The bottom cap, after having been dried as above, is pressed firmly into place, the top cap placed into position and titration commenced.

At first the formalin is added slowly so as to allow it to seep between the organisms, and also to prevent the formation of air bubbles and air pockets. Once the plankton has been covered with formalin the rate of flow may be increased. Again it is advisable to hold the cylinder at a slight angle until the level of the

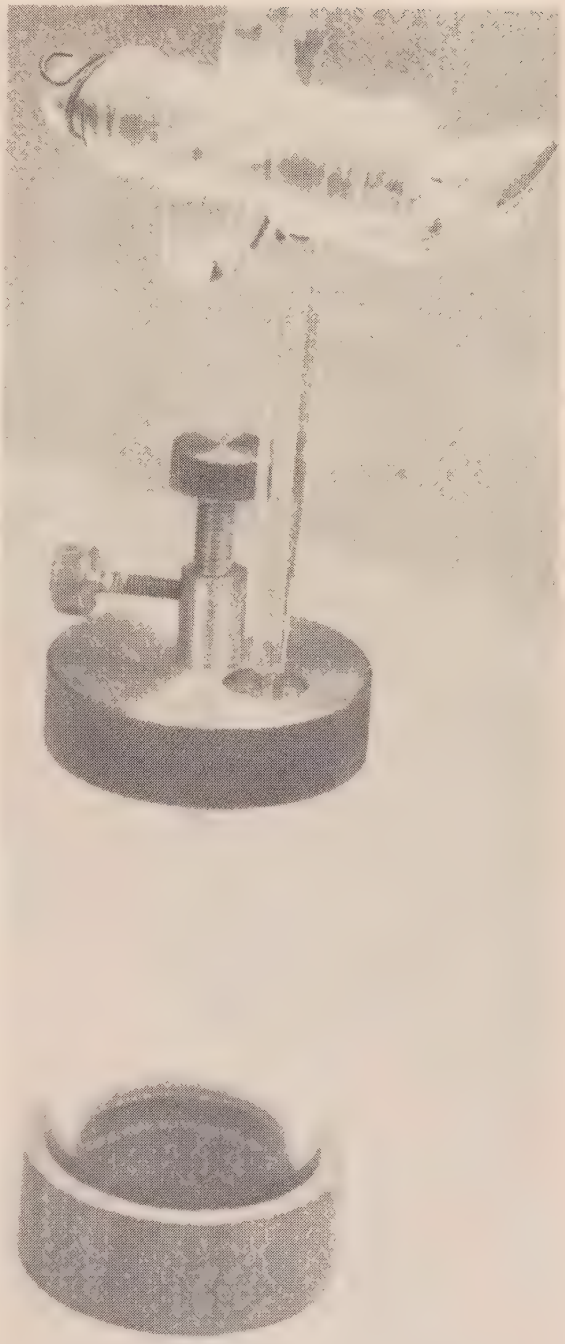

Fig. 3: The instrument ready for calibration.

formalin is approximately 10 mm from the tip of the tapered rod. The flow of formalin is halted and the whole instrument is tapped squarely on the base of the burette stand to remove any small air pockets or bubbles. This can be done by simply raising the instrument a few millimeters and dropping it squarely. (Depending on the volume of plankton it may be necessary to do this more than once during volume determination). The formalin is then introduced slowly until the top of the meniscus is almost touching the tapered rod. After ensuring that the meniscus is evenly formed, the formalin is added drop by drop until the surface just touches the tapered rod. The volume of liquid used is then read off the burette and subtracted from 50 ml to give the volume of liquid displaced by the plankton.

Next, the top cap is removed and the sample poured directly into a specimen tube. If the capacity of the tube is less than 50 ml the bottom cap can be removed, the formalin drained, and after replacing the cap the required amount of formalin is added and the sample transferred to the specimen tube. The remaining plankton is washed off the walls of the cylinder with a jet of formalin from a squeeze bottle. Occasionally small crustacea stick to the gauze but are easily removed with a fine pair of forceps. The whole instrument is then washed thoroughly with a rattail brush.

After a number of samples have been treated, oil from certain crustacea will form a very fine film on the inside walls of the cylinder. As this seriously affects the proper formation of the meniscus, the instrument has to be washed in a soap solution.

The instrument described above proved to have a number of advantages over the original design. By using perspex instead of glass for the cylinder, the instrument becomes extremely tough and practically unbreakable, thus rendering it ideal for field work. The use of perspex also allows the netting to be permanently fixed in position thus facilitating easy and quick hermetical sealing by the bottom cap. This greatly increases the speed with which volume determinations can be carried out. However, by fixing the netting in position, the instrument is limited to measuring one type of sample only which is not the case in the Yashnov meter. This necessitates the construction of a battery of similar instruments to cope with different mesh sizes.

The instrument has also shown that it is possible to measure large numbers of samples both quickly and accurately. Depending on the size and type of sample, 10 to 15 determinations can be accomplished in one hour. Repeated volume determinations on the same sample have shown the accuracy to be very high. The only real danger of introducing an error is in the stage of dryness reached immediately prior to the actual determination. As stated previously it is essential that a standard be set and maintained. For larger samples this can be difficult but is soon overcome with practice.

The instrument and method described above proved to be most effective with pure crustacean samples but some difficulty was experienced when attempting to determine the volume of samples containing large numbers of tunicates, coelenterates etc. This was due mainly to large volumes of interstitial fluid, fluid held by the organisms themselves and the small surface draining area of the netting. It would appear that the only method of overcoming these difficulties is to construct a volume meter with an inverted funnel-shape having a large draining area at the bottom. This would afford more efficient drainage and still permit the last few millilitres of solution to be run in with accuracy.

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OCEANIC CIRCULATION OFF SOUTH AFRICA

L. V. SHANNON

This account is a synopsis of hydrological conditions around South Africa based on data collected during the past seventeen years. The area has been divided into several distinct oceanographic regions, and the circulation pattern of the water masses associated with each region is described.

The research work of the Division of Sea Fisheries has for many years included the regular monitoring of the physical and biological environment of marine fauna of commercial importance. Since 1950 some eleven thousand oceanographic stations, situated within two hundred miles of the coast of South Africa, have been occupied by ships of the Division. This report summarises the findings of these hydrological observations and is augmented by data from six deep-sea cruises into the Atlantic and Indian Oceans. The latter cruises were undertaken during the period 1961 to 1966 and covered the area bounded by latitudes 20°S and 47°S and longitudes 2°E and 58°E (Fig. 1).

In this discussion of oceanic circulation, the nearshore region has been arbitrarily taken as the area of ocean lying within 200 miles of the coast of South Africa and it includes the Agulhas and Benguela Current systems. The offshore region is considered as that zone lying beyond the 200 mile limit and it comprises parts of the South-west Indian Ocean, the Subtropical Convergence, the Sub antarctic area, the Agulhas-Atlantic mixing area and the South-east Atlantic Ocean.

THE NEARSHORE REGION

The near-shore region can be divided into two areas, namely the West Coast region and the East Coast region; the Cape of Good Hope (Cape Point) is considered to be the effective division between the East and West Coast regions. The northwardflowing Benguela Current is associated with the latter area, whereas the Agulhas Current flows in a south-westerly direction along the East Coast. A nearshore area of mixing between Agulhas and Atlantic Ocean water exists, but this is best considered in the discussion of the offshore circulation pattern. The surface currents are shown in Figure 2.

AGULHAS CURRENT SYSTEM

Prior to 1950, data on the Agulhas Current were relatively scarce (see Clowes 1950), but in the interim, several lines of stations have been worked across it at various times by *R.S. Africana II* and *S.A.S. Natal.* Orren (1963, 1966) and Darbyshire (1964) have contributed greatly to our understanding of the Agulhas Current.

The Agulhas Current is a narrow, fast-flowing body of water of Tropical origin, its surface temperature and salinity (21° - 25°C and 35.2°/$_{oo}$ – 35.5°/$_{oo}$ respectively) placing it in the Tropical Surface Water category. The causes and probable fluctuations of the current have been described in detail by Darbyshire (1964). In support of Darbyshire's findings Shannon (1966) noted that the penetration of Agulhas Water into the West Coast was most marked during late summer/early autumn and least marked during late winter/early spring.

From data available it appears that the main body of the Agulhas Current, detected as shallowing tongues of warm water, varies in width from approximately 20 to 100 miles. It follows the general direction of the continental shelf fairly closely, although inspection of several years' data revealed that its distance from the coast was rather variable. At 30° the Agulhas Current flows close inshore with velocities usually between one and two metres per second. At latitude 34°S the major part of the Current starts to veer away from the coast, being progressively deflected by Coriolis force. Before reaching longitude 20°E the main body of the Agulhas bends southwards, eventually turning eastwards to become the Return Agulhas Current. Some Agulhas Water, however, does penetrate into the West Coast region not as true Agulhas Water, but in a mixture with Atlantic Ocean waters (Shannon 1966).

Current strengths deduced from dynamic computations tended to be on the low side, seldom exceeding 60 cm/sec. whereas observations of ship's drift indicated velocities between 1 and 2 m/sec. It has been concluded that the Agulhas Current System is not merely a surface phenomenon, but extends to considerable depths. The fact that the Current closely follows the isobaths is a further indication of uniform current direction over the entire water column.

On the western edge of the Agulhas Current, there is usually a strong uplift of Antarctic Intermediate and Central Water due to the dynamics of the current system. West of *circa* 30°E moderately strong upwelling periodically occurs inshore and this colder water may be associated with the intermittent counter-current which has been reported by ships. The strength and direction of this counter-current appear to be extremely variable.

An eastward-moving counter-current lying seaward of the Agulhas Current was reported by Orren (1966)

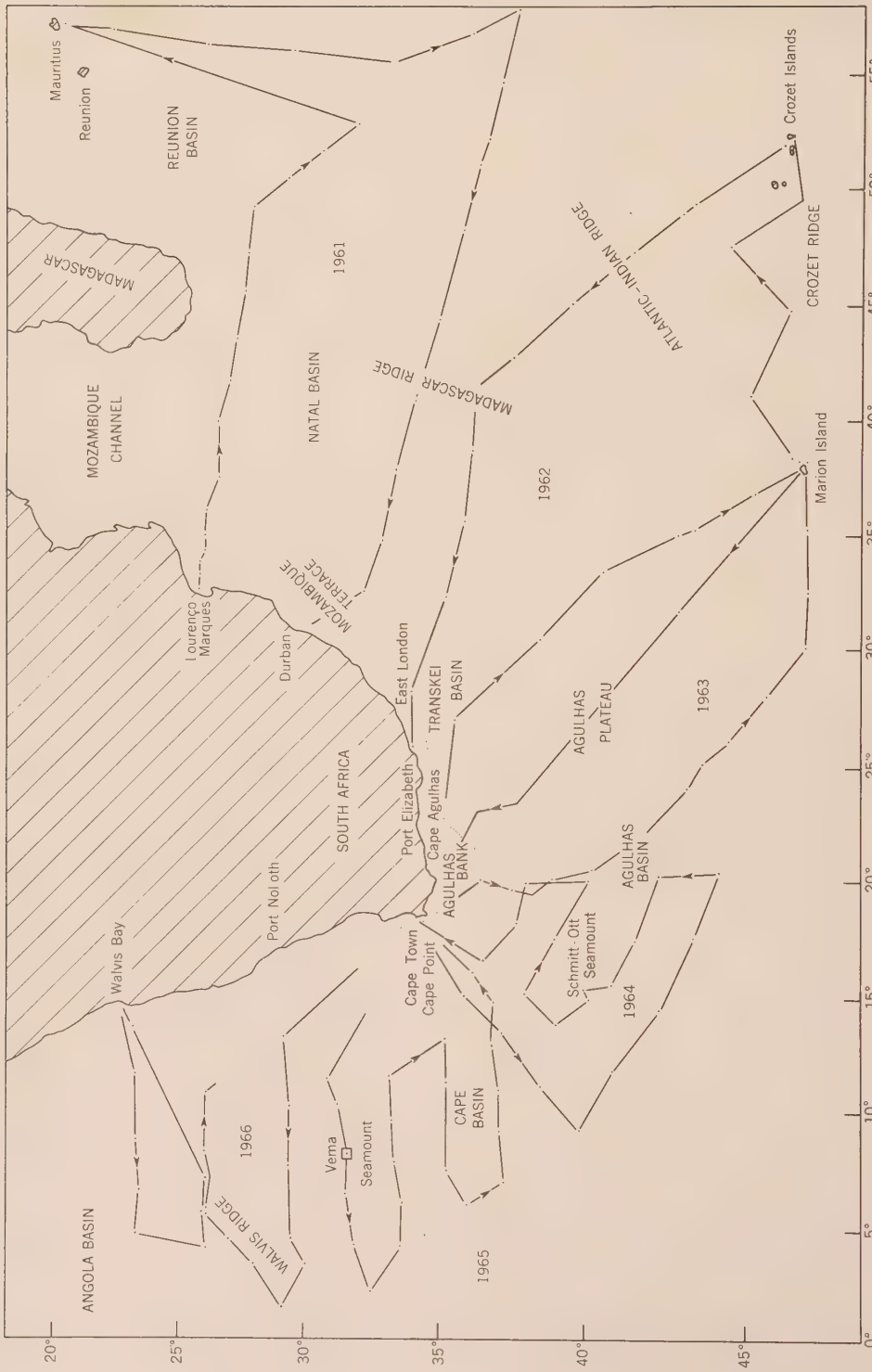

FIG. 1. DEEP-SEA CRUISES OF AFRICANA II - 1961/1966.

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who found that it had a salinity equal to that of the main body of the Agulhas, but a temperature 3°C lower. A similar observation was made on board *R.S. Africana II* during July 1967 when a temperature drop in excess of 2°C in one mile was recorded on crossing the Agulhas Current sixty miles south-east of Port Elizabeth. This phenomenon was accompanied by a salinity increase of *circa* 0.1°/oo. Further observations would be required to establish whether or not this counter-current is a permanent feature of the Agulhas Current System.

BENGUELA CURRENT SYSTEM

The Benguela Current may be regarded as the cool upwelled water found within 100 sea-miles of the West Coast between 15°S and 34°S. The warmer water lying to the west of this limit and forming part of the general anticyclonic circulation in the South Atlantic Ocean, is the South-east Trade Wind Drift. Because of the wind regime and resulting cold current, much of the land lying along the West Coast is desert or semi-desert. The cool coastal water condenses the moisture from the sea-breezes, resulting in the coastal region north of the influence of the belt of the Westerly Winds being arid.

The flow strength of the Benguela Current is dependent on the degree of upwelling along the West Coast. Stander (1964) demonstrated that upwelling along the West Coast north of *circa* 29°S was at a maximum from August to October and a minimum from January to March, while Shannon (1966) showed that, near latitude 29°S, upwelling occurs throughout the year; south of 29°S upwelling reaches a peak during December to February and a minimum from July to August. Thus the Benguela Current System is composed of two parts, with latitude 29°S as the approximate dividing line.

The temperature and salinity associated with periods of maximum upwelling in the Benguela Current may be as low as 9°C and 34.6°/oo respectively (Shannon 1966; Stander 1964). Generally speaking there is a gradual westward increase in temperature and salinity, until at about 200 miles from the coast typical South Atlantic Subtropical Water predominates. The presence of a horizontal salinity discontinuity noted by Hart and Currie (1960) was confirmed by Shannon (1966). This discontinuity was not very marked in the south where it lay *circa* 50 miles offshore, but was more noticeable north of 32°S, and is considered as the western boundary of the Benguela Current.

The Benguela Current, being partly a wind drift and partly a gradient current, is typical of an eastern boundary current. In general it flows northwards, roughly following the isobaths between latitudes 34°S and 23°S while north of 23°S it tends to veer away from the coast. Inspection of the temperature, salinity and dynamic height distribution presented by Stander (1964) shows that water movements in the area north of 23°S are very variable. From time to time warm Subtropical Surface Water has penetrated southwards into the region north of Walvis Bay. This happened on an unprecedented scale during 1963 and had a most adverse effect on the spawning of pilchards and the oil yield of the fish (Stander 1964).

The observed rate of flow of the Benguela Current is variable but is usually between 25 cm/sec and 50 cm/sec (Hart & Currie 1960; Stander 1964; Shannon 1966). Velocities computed from the dynamic height distribution are somewhat lower than observed values, indicating that, as in the case of the Agulhas Current, the Benguela is not merely a surface phenomenon.

Close inshore along the West Coast a southward-moving counter-current has periodically been recorded. In the area between 34°S and 30°S its frequency was highest during the winter months (Shannon 1966), a fact which has been confirmed by measurements of ship's drift and by drift card returns.

Upwelling in the Benguela Current causes an elevation of Atlantic Central Water, and although the depth affected by upwelling is as a rule limited to 300 m (Hart & Currie 1960; Stander 1964; Shannon 1966), water originating from depths greater than 400 m offshore has occasionally reached the surface inshore.

The marked southward flow at a depth of *circa* 200 m in the Benguela Current off South West Africa, reported by Stander (1964), did not penetrate much further than 23°S and Shannon (1966) found no indication of this compensating flow in the region south of latitude 29°S.

The Antarctic Intermediate Water in the Benguela Current System was traced as moving slowly northwards at depths ranging from *circa* 800 m in the south to *circa* 600 m in the north. At no time was there any evidence of Antarctic Intermediate Water reaching the sea surface, although the depth of the core was modified appreciably by eddies and upwelling of overlying Central Water.

THE OFFSHORE REGION

As mentioned earlier, the offshore region is considered as that area lying further than 200 miles from the coast and can be divided into five main oceanographic areas, each with its characteristic water masses and circulation.

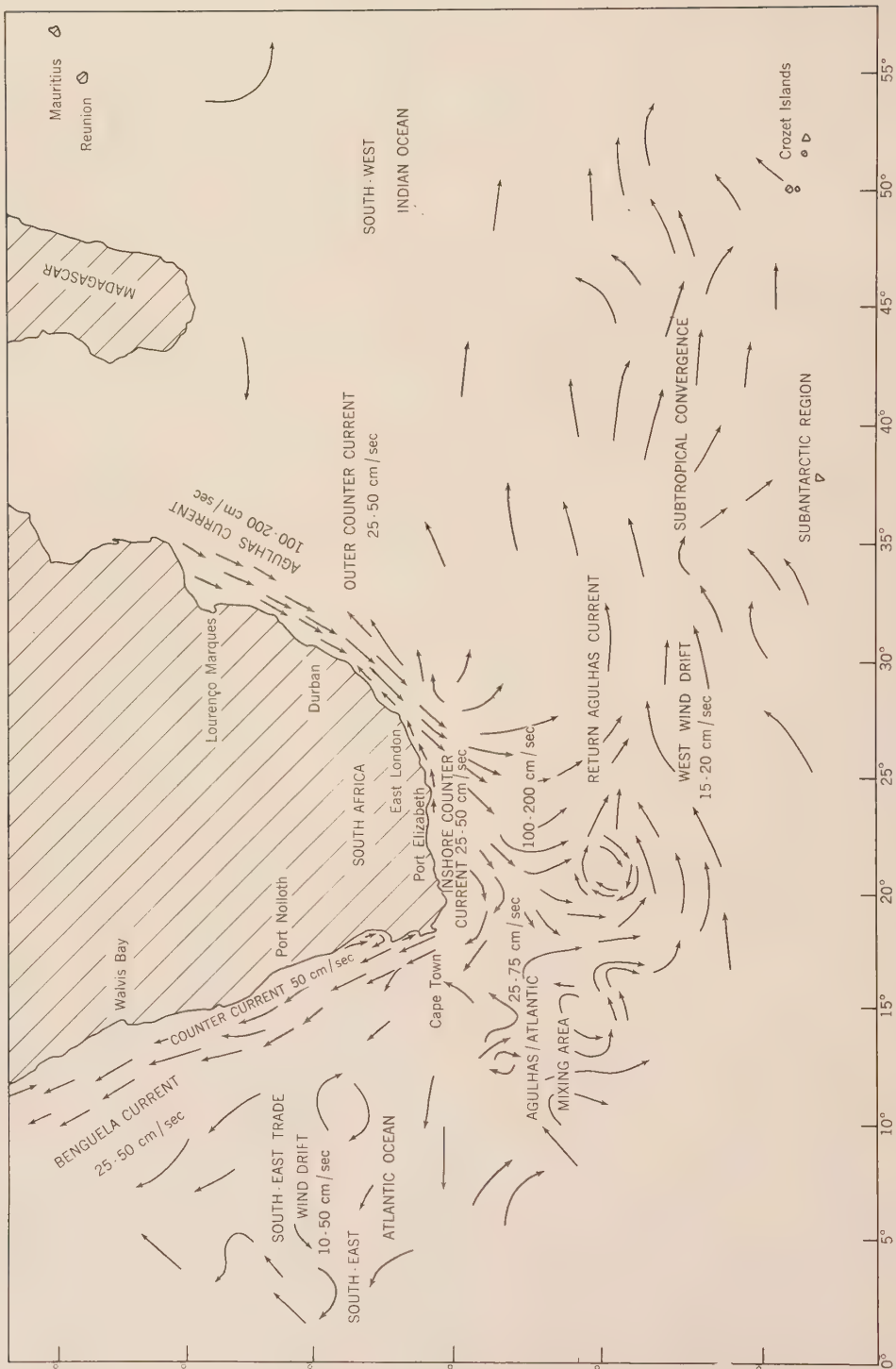

FIG. 2. SURFACE CURRENTS ROUND SOUTH AFRICA

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SOUTH-WEST INDIAN OCEAN

Data from this area do not permit a detailed study of currents, but some idea of the movement of the various water masses was nevertheless obtained.

Tropical Surface Water was present in the offshore area north of *circa* 25°S and the movement of this warm, poorly saline water (*circa* 25°C, 35.3°/₀₀) was sluggish. This water mass was separated from Subtropical Surface Water by the poorly defined Tropical Convergence, lying near latitude 25°S in the are east of Malagasy.

Subtropical Surface Water was present as a warm saline layer (*circa* 15°C - 23°C, 35.3°/₀₀ - 35.7°/₀₀) in the area between 25°S and 42°S and data extracted from ship's drift observations indicated that its movement was anticyclonic and generally slow. A strong south-eastward flow of 1 m/sec was recorded at *circa* 35°S, 28°E, in water associated with the Agulhas Current System. East of 28°E, along a line of stations approximately following latitude 35°S, a northward movement of about 25 cm/sec was noted by Orren (1966). This flow intensified westwards to became the counter-current mentioned earlier. In the West Wind Drift near the Subtropical Convergence, the surface flow was eastwards, but the velocities were lower than expected. However, several plastic drift cards released at 35°S, 20°E, and subsequently recovered from the west and south coasts of Australia, indicated an approximate easterly movement of about 16 cm/sec for the West Wind Drift in the Indian Ocean.

Subsurface currents, detected by a salinity maximum, were in evidence in the South-west Indian Ocean in the area north of 30°S. The core of maximum salinity was normally encountered between 200 m and 250 m, and maximum salinities in excess of 35.5°/₀₀ were recorded. Orren (1963) found that sinking took place in the area south of 33°S, the salinity maximum core dipping slowly northwards. Orren also found that the core was depressed somewhat on the eastern side of the Agulhas Current, due to sinking of the Subsurface Water under the main body of the Agulhas.

Central Water occurred in the entire Subtropical region as a layer of linear T/S relationship, separating the Subsurface and Antarctic Intermediate layers, i.e. between 200 m and 800 m. The mode of formation of the Central Water found in the Indian Ocean has been investigated by Orren (1966), who considered the centre of this water mass as having a temperature of 11°C and a salinity of 35.0°/₀₀. The general movement of Central Water in the South-west Indian Ocean was northerly. Orren (1966) thought it likely that a penetration of Central Water from the Atlantic Ocean into the Indian Ocean occurred offshore south of Cape Agulhas, while Shannon (1966) found indications of Indian Ocean Central Water penetrating westwards into the Atlantic closer inshore. Both authors arrived at their conclusions after considering oxygen data in conjunction with temperature salinity and sigma-t values. In the area under the influence of the Agulhas Current, the flow of Central Water was cyclonic.

Between the Central Water and the Deep Water lies the Antarctic Intermediate layer, which is characterised by a salinity minimum. In the South-west Indian Ocean the core of the Antarctic Intermediate Water has a temperature of 4°C - 5°C and a salinity of 34.4°/₀₀-34.5°/₀₀ and lay at depths between 900 m and 1,300 m. In the South Atlantic, by comparison, its core salinity was 0.1°/₀₀ to 0.2°/₀₀ lower and it was encountered 200-300 m shallower. The movement of Antarctic Intermediate Water, derived from the salinity, temperature and oxygen content at the salinity minimum, and the distribution of these various parameters along the appropriate sigma-t surface, agreed well with the dynamic topography of the 1.000 decibar surface given by Visser & Van Niekerk (1965). Orren (1966) noted a strong northerly flow of Intermediate Water in the Natal Basin, which weakened in the Moçambique Channel. The Atlantic-Indian Ridge also appeared to deflect part of this northward-moving water while near the Agulhas Current area, the movement of the Antarctic Intermediate Water followed the south-westerly trend of the overlying layers closely. Data on the area of interaction between this south-westerly motion and the general northerly flow of the Intermediate Current are unfortunately scanty.

Deep Water, corresponding to the salinity maximum of *circa* 34.75°/₀₀ - 34.80°/₀₀ lay at depths usually between 2.500 m and 3.000 m. The small variations in the properties of Deep Water rendered the tracing of this water mass difficult. There are indications of an easterly movement of North Atlantic Deep Water from the Atlantic into the Indian Ocean south of South Africa, and the Agulhas Plateau appears to split this flow, one component moving northwards in the Natal Basin and the other following the coast immediately to the east of the Agulhas Current. In the Moçambique Channel, Orren (1963) found evidence of the southward penetration of warmer, slightly less saline North Indian Deep Water overlying the Atlantic Deep Water at a depth of about 1.600 m. He considered that the inshore stream of Deep Water is deflected by the Moçambique Terrace and returns southwards with some admixture of North Indian Deep Water.

SUBTROPICAL CONVERGENCE REGION

The Subtropical Convergence, the boundary between the Subtropical and Subantarctic regions, lay at *circa* 42° S ± 1° latitude in the area between 15° E and 50° E longitude, but its position seems to be modified significantly by the eddies of warmer water lying immediately to the north.

On the line of stations worked between Port Elizabeth and Marion Island the Subtropical Convergence was marked by a drop in temperature from 18.5°C to 7.5°C in 90 miles and a corresponding decrease in salinity from 35.5°/₀₀ to 33.8°/₀₀ (Orren 1966). Ship's drift observations showed a southward movement of Subtropical Water in this area with a resultant intensification of the Convergence.

The temperature and salinity distribution at 50° E confirmed the strong northward penetration of Subantarctic Water into the region north of the Crozet Islands. This northerly flow is thought to be due to the shallowing influence of the Crozet Ridge on the West Wind Drift.

The sinking and mixing in the vicinity of the Subtropical Convergence and the subsequent formation of Central Water was illustrated by Orren (1966), who postulated a fairly complex cellular circulation. He reported that mixed water which had sunk at the Convergence spread northwards at about 340 m for 200 miles, whereupon it mixed with upwelled Antarctic Intermediate Water. This mixture then sank northwards to form Central Water.

SUBANTARCTIC AREA

Owing to the limited number of oceanographic observations made by the Division of Sea Fisheries in this area, no discussion of the circulation can be attempted here.

The temperature and salinity of Subantarctic Surface Water ranged from 4.2°C to 7.5°C and 33.69°/₀₀ to 33.82°/₀₀ respectively. In the region between Marion Island and the Subtropical Convergence a slight southerly drift was noted, while further east the flow was north-easterly, intensifying eastwards over the Crozet Ridge. Orren (1966) stated that thermoclines were generally absent in the Subantarctic Water, but noted that there were many slight inversions associated with subsurface currents and intense vertical mixing.

AGULHAS/ATLANTIC MIXING AREA

The inshore area of mixing between Atlantic and Agulhas Water can be demarcated approximately by the region between the 21° E meridian and a line running in a west-south-westerly direction from Cape of Good Hope (Shannon 1966). Hydrological data from a cruise into the offshore area in the vicinity of the Schmitt-Ott Seamount showed that the boundaries of the inshore mixing area could be extended as far as the Subtropical Convergence (± 42° S).

Clowes (1950) mentioned the existence of several large eddies south of South Africa. A large eddy centred around 40° S, 20° E and extending to depths in excess of 1.500m is evident on several of the charts presented by Dietrich (1935), while other smaller eddies are apparent from the *Discovery* and *Meteor* data. During March 1964 a large anticyclonic eddy, centred around 40° S, 15° E and extending to depths exceeding 1.000 m (possibly as deep as 3.000 m) was observed. It appears, therefore, that the eddy which is presumably caused by the interaction between the Agulhas Current and the West Wind Drift is of a permanent nature although some seasonal shift in its position would be expected. The effect of the eddy was to bend the Subtropical Convergence southwards, which resulted in the production of very sharp horizontal temperature and salinity gradients across the Convergence.

The area surveyed during 1964 was characterised by other smaller eddies and instrusions of warm and cold water, indicating the turbulent nature of this complex oceanographic region. It is quite possible that some of the eddies were associated with the numerous seamounts of the area.

The circulation pattern of the underlying Central Water and Antarctic Intermediate Water closely resembled that of the surface. In fact, the large anticyclonic eddy mentioned earlier was more marked in the deeper water layers. The general movement of the Antarctic Intermediate Water which lay at variable depths between 500 m and 1,400 m, was anticyclonic, although a northerly component was apparent in the area west of 13° E.

The nearshore area of mixing between Agulhas and Atlantic Water was discussed by Shannon (1966), who found that the warm surface water that penetrated into the West Coast region during summer and autumn was not pure Agulhas Water but rather a north-westerly flowing component of water from the mixing area. It is also likely that some Central Water of Indian Ocean origin penetrates at sub-surface depths into the Atlantic Ocean south of the Agulhas Bank, but it is unlikely that much Antarctic Intermediate Water from the Indian Ocean penetrates into the Atlantic.

The mixing area apparently acts as an effective buffer between the Atlantic and Indian Oceans.

SOUTH-EAST ATLANTIC OCEAN

The general circulation in the South Atlantic is anticyclonic and relatively simple. The region under

consideration, namely the South-east Trade Wind Drift, lies to the west of the Benguela Current (and forms part of this circulation pattern).

The surface water present over the entire region was Subtropical Surface Water having a typical temperature and salinity of *circa* 20°C and 35.6°/oo respectively. During the two cruises undertaken by the Division of Sea Fisheries into this area, the surface thermohaline structure was very uniform, the iso-lines running approximately meridianally.

In the Cape Basin Region numerous eddies were evident and may have originated in the Agulhas/Atlantic mixing area and subsequently moved northwards before finally petering out. Examination of T/S data lends support to this theory. A cyclonic eddy was present over the Vema Sea-mount, with upwelling taking place to subsurface depths. Pisa tube current indicators used over the Seamount showed no measurable currents in contrast to the strong variable currents reported by Simpson & Heydorn (1965). Although hydrological data on the Vema Seamount are lacking, it is considered that the eddy was in fact due to the presence of the Seamount and did not originate from mixing areas to the south.

Over the Walvis Ridge the surface currents followed the isobaths very closely. Shannon & Van Rijswijck (1969) noted that, although the agreement between ship's drift and dynamic analysis (using the 1000 decibar surface as reference level) was fair, the latter method tended to underemphasise the actual current speed. Over the Ridge itself the general movement was in a north-easterly direction but between latitudes 27°S and 26°S a strong westerly component was recorded. This movement was evidently caused by the shallow portion of the Walvis Ridge at about 26°S, 6°E, over which an anticyclonic eddy was present.

Subsurface currents were detected in the region north of latitude 30°S. Shannon & Van Rijswijck (1969) observed that the subsurface current had a marked easterly component and was strongest in the north of the region.

Sandwiched between the subsurface and Antarctic Intermediate layers was Central Water corresponding to the linear portion of the T/S curve between about 6°C, 34.4°/oo and 16°C, 35.4°/oo. The slope of the T/S curve for Atlantic Central Water is steeper than for Indian Central Water (Orren 1963; Shannon 1966).

In the area under review, Central Water was detected at depths ranging from 50 m to 700 m. Eddies were in evidence in this water mass in the Cape Basin area, while over the Walvis Ridge the movement of Central Water showed a similar circulation pattern to the Subtropical Surface Water. Shannon & Van Rijswijck (1969) reported a westerly flow of 15 cm/sec between 26°S and 27°S by considering the distribution of dynamic heights for the 200/1,000 decibar surface.

In the South-east Atlantic Ocean the salinity minimum core was present at depths ranging from 600 m to 1,100 m, the temperature and salinity being within the ranges 3.5°C - 5°C and 34.3°/oo - 34.4°/oo respectively. The general movement was from south-west to north-east in the area south of about 27°S while between 26°S and 27°S there was a westward component over the Walvis Ridge. Several eddies were present in the Antarctic Intermediate layer and had the effect of modifying the local circulation pattern.

Deep Water was detected as a layer underlying the Antarctic Intermediate Water at a depth in excess of 2,000m and had T/S values of about 3°C and 34.9°/oo. The movement of the Deep Water was southwards, sinking from *circa* 2,000 m at 16°S to 3,000m at 32°S.

Although the Division of Sea Fisheries has made few measurements of Bottom Water, data extracted from Fuglister (1960) indicated that the northward flow of South Atlantic Bottom Water at *circa* 4,000m was fairly effectively blocked by the Walvis Ridge, while in the Angola Basin southward-moving North Atlantic Bottom Water was present as a layer of relatively high temperature and salinity.

Observations made by the Division in recent years are generally in good agreement with those made by the *Discovery* and *Meteor* several decades ago, indicating the stable nature of the circulation pattern in the South-east Atlantic Ocean.

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ANALYSIS OF PARTICULATE MATTER AND NUTRIENTS IN SEA-WATER

S. A. MOSTERT

The bulk of the biomass in sea-water is in the form of microscopic particles and consists largely of phytoplankton, organic detritus and inorganic material. The phytoplankton consists of all the passively floating plants of the sea, its chief components being the diatoms and the dinoflagellates. Phytoplankton organisms as producers of the primary food supply through photosynthesis, are of paramount importance because they constitute the first links in the marine food chain which terminates in the larger fishes and marine mammals.

Phytoplankton production (primary production) is generally understood to be the amount of organic matter produced under a unit area of sea-surface or in a unit volume of sea-water during a given period of time (Sverdrup 1942). This production is dependent upon radiant energy for the process of photosynthesis and it requires inorganic nutrients such as phosphates, nitrates and iron in solution in the water. It also relies upon physical or biological factors which control the availability of these dissolved substances. Thus phytoplankton production is influenced by certain physical, chemical and biological parameters which directly affect the metabolism or the actual survival of the organisms themselves. For instance, the rate of metabolism is much increased with rise in temperature, whereas salinity and pH have an effect on the production rate of phytoplankton. The control of growth is expressed in Liebig's law which states that growth is limited by the factor that is present in minimal quantity (Sverdrup 1942).

Data on phytoplankton may be obtained by direct measurement (census), by pigment analysis of the plant population or by means of chemical analysis of the water in which it grows. At present the only rapid chemical method known for estimating living plant material in the particulate organic matter of sea-water, is the determination of characteristic plant pigments, namely, the chlorophylls, carotenes, and xanthophylls. Unfortunately, the amount of organic substance associated with a given quantity of plant pigments is very variable, depending on the type of phytoplankton and its state of nutrition. Decay or grazing by zooplankton on phytoplankton causes a preferential destruction of chlorophyll and abnormally low ratios of chlorophyll to total carotenoids probably indicate a heavy concentration of plant detritus (Riley & Skirrow 1965).

The direct census method is essential to detailed analysis of the constituents of the phytoplankton communities and for arriving at an understanding of the factors operating in controlling the production of the different ecological types. Any sample is only a measure of the standing crop, that is the density of individuals (total volume) or weight present at the moment of sampling. The common method of phytoplankton analysis consists of centrifuging or filtering a known volume of water and directly counting under the microscope the number of cells of species thus concentrated. The population density is recorded as the numbers of cells of the various species per litre or per cubic metre of the water. It is, however, extremely difficult to arrive at accurate estimates of volumes or weights of organic matter only through plankton counts, since diatoms and dinoflagellates vary greatly in size and organic content; indeed a large proportion of the diatoms consist of inorganic material which forms their siliceous cells.

Measurements of "settled volumes" and "displacement volumes" are sometimes made, but all measurements give only relative values which merely reflect the major differences. It is, for instance, not always possible to drain off the water completely; thus the volume may include the water residue and also inorganic structures from the organisms.

Because direct plankton measurements are inadequate for arriving at figures of total vegetative (organic) matter in the standing crop, or of the total production for a given period of time, chemical analyses have been made of the essential nutrients consumed by the plants. Changes in the concentrations of these plant nutrients coincident with plant growth are highly useful as indices of production. Redfield (1934), Cooper (1938) and others have demonstrated the existence of a rather constant ratio between carbon, nitrogen and phosphorus in the organic content of mixed plankton. The ratios C : N : P = 41 : 7.2 : 1 by weight and 106 : 16 : 1 by atoms, are also in close agreement with the proportions of these elements in sea-water. Therefore the measurement of a decrease in any of these elements present in a mineralized state in sea-water could reasonably be supposed to indicate an equivalent incorporation into organic material during synthesis of carbohydrates or proteins. The carbon content is the best single property with which to measure the standing crop of phytoplankton in nature and it has been found that the carbon content of marine organisms is remarkably constant between 45 per cent and 55 per cent (Riley & Skirrow 1965).

Although the total phosphorus and nitrate content of a water column is a qualitative index of relative fertility, especially in shallow water where the euphotic zone extends nearly to the bottom, the rates

of supply of nutrients by mixing and regeneration account for the major part of the nutrient cycle of plant production.

During the winter season when phyto-plankton growth is at a minimum, vertical mixing, which is greatest at this time, produces a nearly uniform distribution of plant nutrients, such as phosphates, nitrates and silicates, throughout the water column. As the result of the spring bloom these nutrients are rapidly depleted to low values which persist throughout the summer and most of autumn (Kethcum 1958).

Silicates, used in the formation of the siliceous shells of diatoms, show seasonal fluctuations and also vertical distribution correlated with phytoplankton activity.

The amount of total carbohydrate known as "crude fibre", gives a qualitative indication of the detritus to plant ratio since the concentration of crude fibre is high in detritus (± 70 per cent) and low in living phytoplankton (± 15 per cent). The amount of protein also gives an indication of the living as distinct from the detrital matter (Krey *et al.* 1957).

During winter there is a maximum accumulation of phosphate in the sea in the higher latitudes. This phosphate, when returned to the euphotic zone, constitutes the available supply for the next spring growth of plants. Not only do the plants vary in their ability to utilise this phosphate, but the supply also varies from year to year owing to the nature of the water flowing into the region. This has a profound influence on both plant and animal production. Years of low phosphate are correlated with scarcity of plankton and poor production of young fish (Sverdrup *et al.* 1942).

The utilization of nitrate by the growing phytoplankton also gives an index of seasonal production.

The most satisfactory method for the measuring of the standing crop of phytoplankton, once this is separated from detritus and animal matter, is to oxidize the plant material back to carbon dioxide, from whence it originated as a result of photosynthetic reduction. Of all the gross measurements of the living tissue in the plankton this is probably the most realistic and bears the closest relation to the amount of purely organic material in the plants.

Apart from carbon many other elements could be used as a measure of standing crop, provided that the amounts of these elements in the plant cells were fairly constant and accurately known (Strickland 1960)

Plants obtain carbon for carbohydrate synthesis from the carbon dioxide dissolved in the water.

$$6\,CO_2 + H_2O = C_6H_{12}O_6 + 6O_2$$

Above the compensation depth so much O_2 is evolved as a by-product of photosynthesis that the water may become super-saturated with oxygen. A measure of this oxygen production provides a means of calculating the amount of carbon that is bound in the organic products.

There is no doubt that water-masses differ in their ability or inability to sustain growth of various organisms. In this respect the most fertile areas of the sea are near the coasts, above shallow bottoms and in zones of water mixing e.g. at the merging of different bodies of water and upwelling (Provasoli 1963). Water masses can be characterized by their peculiar concentrations in organic nitrogen and carbon, besides the usual variations in salinity and temperature (Duursma 1960).

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RED WATER AND MUSSEL POISONING AT ELANDS BAY, DECEMBER 1966

J. R. GRINDLEY and E. A. NEL*

"Red water" or "red tides" have been observed in widely scattered seas throughout the world, mostly in the coastal regions. They are caused by the blooming of usually only one species of plankton which may be a diatom, dinoflagellate, flagellate or blue-green alga. Oceanic red tides may be caused by the blue-green alga *Trichodesmium erythraeum*, whereas various flagellates have been associated, for instance, with the mortality of fish on the Malabar Coast of India (Bhimachar & George 1950).

The great majority of red tides, however, are caused by various species of dinoflagellates. Many of these outbreaks are harmless to marine life, while others cause mass mortality of fish and other marine fauna, and some are the source of paralytic shellfish poisoning in man. Previous records of these two phenomena have suggested that they are distinct; thus those dinoflagellate species which have resulted in mass mortalities of marine fauna have not been involved in mussel poisoning of man, while those species causing toxicity in mussels have not been found to actually harm the mussels. A table illustrating the two distinct effects was published by Grindley & Taylor (1964). Brongersma-Sanders (1948, 1957) summarises our knowledge of mass mortalities by red water in different parts of the world.

Gymnodinium breve on the west coast of Florida (Gunter *et al.* 1948) and *Gonyaulax monilata* on the east coast (Gates & Wilson 1960), are two dinoflagellates which cause the death of marine fauna by means of specific toxins. Non-toxic species cause marine fauna mortalities when they decay in large numbers and deplete the oxygen in the water, e.g. *Gonyaulax polyedra* (Kofoid 1911; Stohler 1959; Reish 1963) and *Gonyaulax polygramma* (Grindley & Taylor 1962, 1964; Nishikawa 1901).

Several different dinoflagellates have been found to be the source of a toxin that causes paralytic shellfish poisoning in man. This phenomenon has been reported from various parts of the world, and in some cases has resulted in the death of humans. Walker (1884) reported that streaks of red water were present in the Gulf of Mexico when the oysters were toxic and poisonous to humans.

Sommer & Meyer (1937) demonstrated that *Gonyaulax catenella* was the source of mussel poison on the coast of California. Woloszynska & Conrad (1939) identified the dinoflagellate *Pyrodinium phoneus* as responsible for the toxicity of mussels in Belgium, during an outbreak which resulted in several deaths.

In 1942, 114 people died from eating shellfish *(Venerupis semidecussata)* from Lake Hamana (Japan) and during the following spring, people were poisoned after eating toxic oysters. The source of the toxin was found to be a dinoflagellate *Prorocentrum* sp. (Nakazima 1965).

In 1945 a large number of people were poisoned after eating various species of shell fish from the Bay of Fundy area (Canada) and the source of the poison was identified as the dinoflagellate *Gonyaulax tamarensis* (Medcof *et al.* 1947).

In 1955, cockles in a lagoon on the west coast of Portugal were found to be toxic, resulting in the poisoning of humans and one death. Large numbers of the dinoflagellate *Prorocentrum micans* were present in the waters of the lagoon at that time, and this species was suggested as the source of the toxin (Pinto & Silva 1956).

In 1961 in Ofunato Bay (Japan) 20 people were poisoned and one died from eating toxic mussels. The source of the toxin is not known (Kawabata *et al.* 1962), but it was thought to be a dinoflagellate species.

Prakash & Taylor (1966) found that *Gonyaulax acatenella* was the dinoflagellate responsible for the toxicity of cockles in the Strait of Georgia in 1965; eating these shellfish resulted in four cases of poisoning and one death.

Red water is a common occurrence around the coasts of South Africa, particularly on the West Coast. Gilchrist (1914) records several early outbreaks that were associated with fish mortalities. Most of the red water blooms around our coasts are caused by the non-toxic dinoflagellate *Noctiluca miliaris*, and in some areas such as False Bay, these outbreaks occur intermittently throughout the year. Grindley & Taylor (1964) also record some species that have caused red water around South Africa.

There have been several cases of mussel poisoning around the coasts of South Africa during the past hundred and thirty years, which in some cases resulted in human deaths. In 1837 a number of people in Cape Town died after eating poisonous fish. In 1888 many people were taken ill and some were believed to have died after eating shell fish during a red water outbreak (Gilchrist 1914). Several baboons, clutching clam shells, were seen lying dead at Simonstown (False Bay) at that time. In 1948 one person died from eating mussels from the Blouberg area. In

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1957 there was one death from mussel poisoning at Tongaat on the Natal Coast, and in 1958 another death as a result of eating mussels from Paternoster.

During recent years in South Africa the only outbreak of red water that resulted in a mass mortality of fish and other marine fauna, occurred in False Bay in March 1962, where the fauna was killed after the decay of dense concentrations of *Gonyaulax polygramma* (Grindley & Taylor 1962, 1964). In February 1967, during a bloom of *Noctiluca miliaris* in Simonstown (False Bay), a number of dead fish were washed ashore, and others were seen gasping at the surface.

During December 1966 red water caused by high concentrations of an apparently unknown species belonging to the dinoflagellate genus *Gonyaulax*, appeared off the West Coast of South Africa. This bloom resulted in the death of hundreds of thousands of White mussels *Donax serra*, as well as a large number of Black mussels *Chloromytilus meridionalis* and many other marine invertebrates including cephalopods and holothurians. Toxicity tests (kindly performed by Professor N. Sapeika of the Pharmacology Department, University of Cape Town), employing the method of Sommer & Meyer (1937), were carried out on the mussels collected from the affected area. These revealed that both the White and Black mussels, including live specimens, were highly toxic.

The *Gonyaulax* responsible for the red water bloom along the West Coast of South Africa and particularly at Elands Bay, has been described as a new species *Gonyaulax grindleyi* (Reinecke 1967). This species may prove to be identical with *Protoceratium reticulatum*, but the arrangement of plates suggests that it would have to be referred to as a *Gonyaulax*.

METHODS

Red Water Samples

At the time of the red water and associated mortality of 21 December 1966, various samples were taken of the red water bloom at Elands Bay as follows (Fig. 1).

1 and 2 – off the rocky point in red water
3 – off the beach in green water
4, 5, 6 and 7 – in a straight line from the beach seawards to a depth of approximately two feet in the red water bloom, in the following order: 4 (shore), 5, 6 (low-water mark) and 7 (in two feet of water).

On 5 January 1967, after the main concentrations of red water had been dispersed, more samples (Fig. 2) were taken at Elands Bay (AI), Lamberts Bay (AII), Laaiplek (AIII) and Stompneus Bay (AIV).

The samples were preserved in 10% neutral formalin. The species in the samples were then counted in twenty squares on a squared, welled slide using the centrifugation method as described by de Jager (1957), and the number of cells/litre calculated. Three counts for quantitative analysis were made on each of these samples.

Samples were also taken at Ysterfontein, Melkbos, Blouberg, Sea Point and Muizenberg during December and January for qualitative analysis (Fig. 3).

Routine Samples

The Division of Sea Fisheries undertakes monthly routine cruises around the coast from Lamberts Bay to Cape Infanta, east of Cape Agulhas. A number of samples taken at three stations on these cruises in the vicinity of the red water outbreak were analysed to determine when *Gonyaulax grindleyi* first appeared in the plankton in that area. The Stations were numbered 20-1 (off Lamberts Bay), 24-1·5 (4·5 miles N.W. of Stompneus Bay) and 28-1 (9 miles west of Jacobs Reef), all being 5-10 miles from the coast (Fig. 2). These samples were of two kinds, namely N50V net samples, taken with a 50 cm diameter net (± 200 meshes to the linear inch) of the *Discovery* type (Kemp, Hardy & Mackintosh 1929) which was hauled vertically from 50-0m; a Nansen-Pettersson water sampler was used to take samples from 10m. Only cells of *Gonyaulax grindleyi* were counted. The N5OV samples were poured into measuring cylinders and allowed to settle for 24 hours before the settled volumes were measured. These samples were then examined for *Gonyaulax grindleyi.*

Mussel Samples

A number of White and Black mussels killed during the red tide were collected, and the gills and gut contents examined microscopically.

At the time of the red water outbreak in December, both living and dead White and Black mussels were collected from various places along the coast from Muizenberg to Lamberts Bay (Fig. 3). After the red water had been dispersed, live White and Black mussels were collected along the West Coast from Melkbos to Strandfontein (Fig. 3) at different times until June 1967. As the toxin is unaffected by extreme temperatures, the mussels were kept fresh by freezing. All the mussel samples were tested for toxicity according to the method described by Sommer & Meyer (1937).

Field Observations

Field observations and collections were made at various times in December 1966 and January 1967. In addition to the material gathered for the analyses described above, notes were made about marine fauna killed by the red water, the distribution area of the

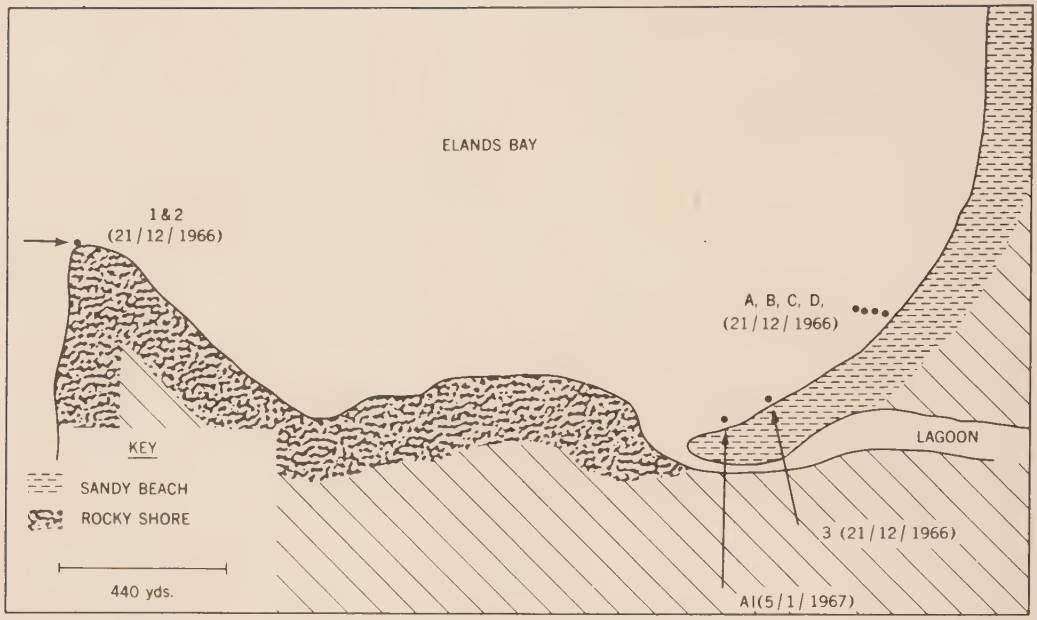

FIG.1. POSITION OF RED WATER STATIONS AT ELANDS BAY

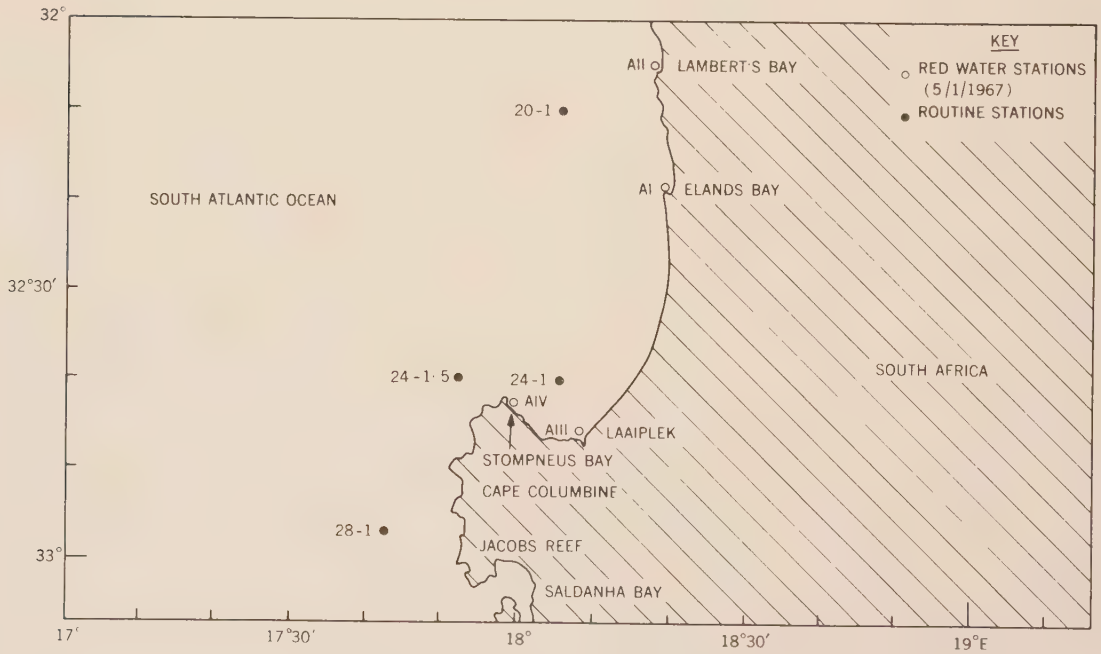

FIG. 2. POSITION OF ROUTINE AND RED WATER STATIONS (JANUARY 1967)

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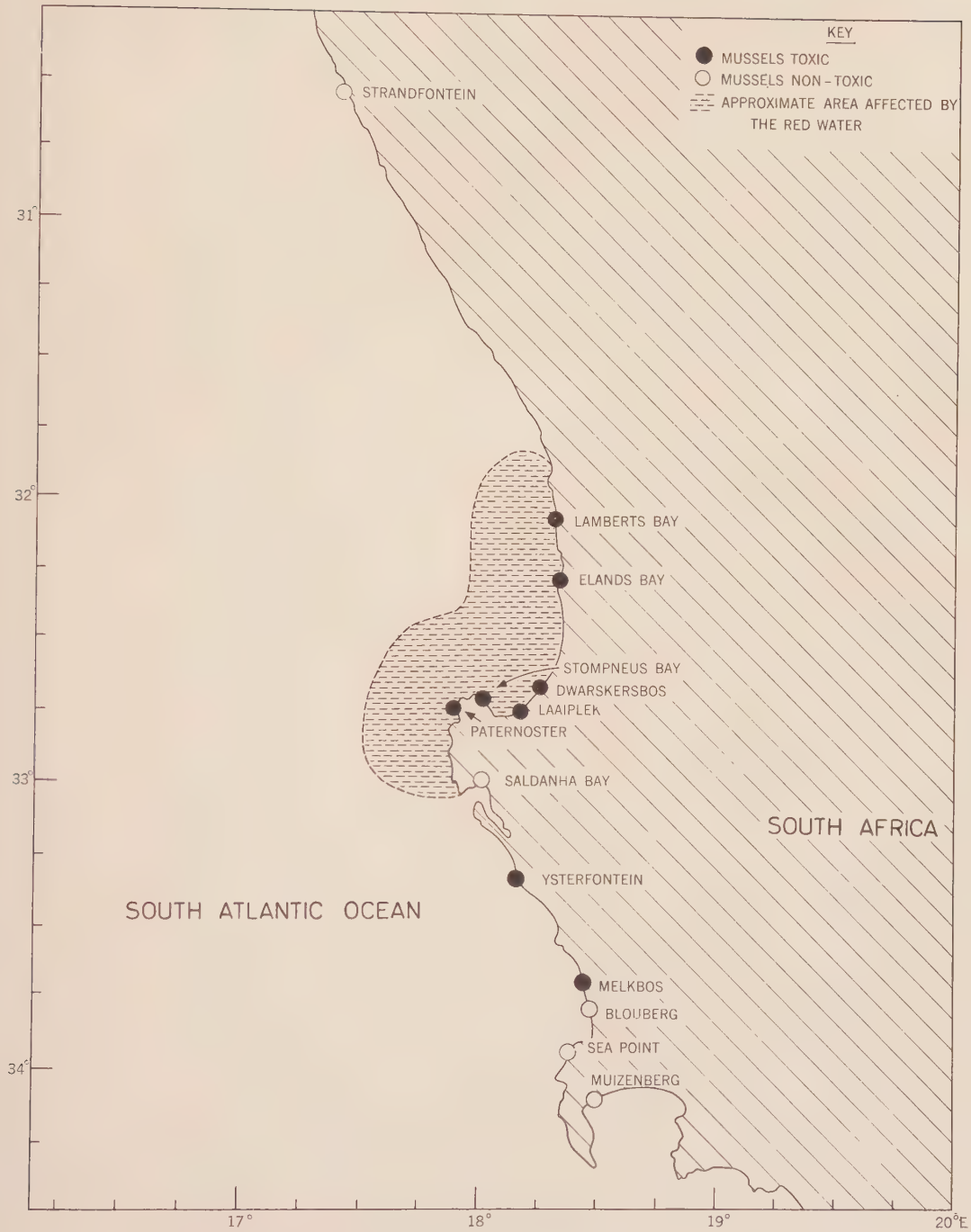

FIG. 3. EXTENT OF RED-WATER BLOOM AND LOCALITIES WHERE MUSSELS WERE COLLECTED

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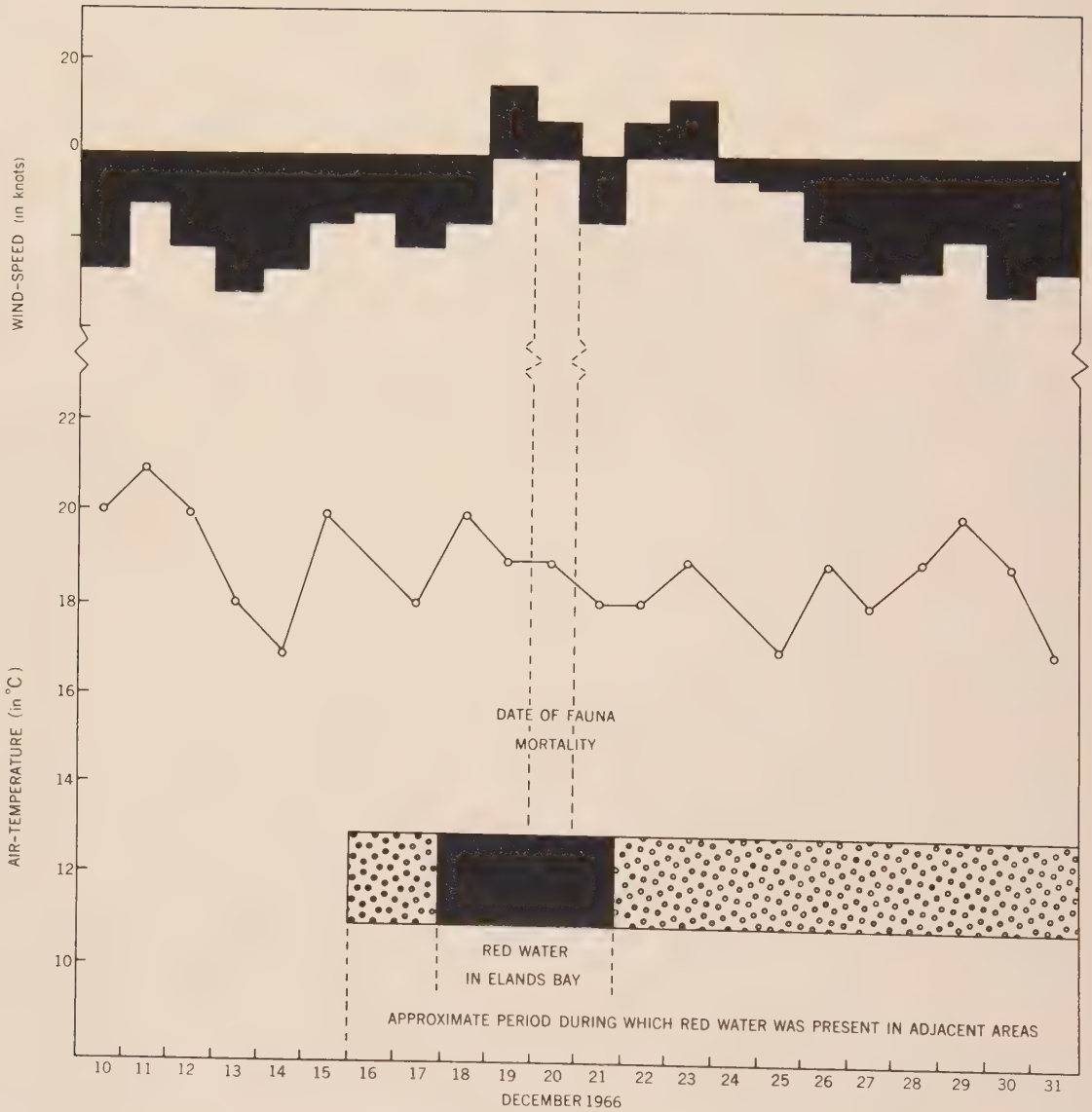

FIG. 4. OCCURRENCE OF RED WATER CORRELATED WITH WIND-SPEED, WIND DIRECTION AND AIR-TEMPERATURE

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TABLE I: HYDROLOGICAL DATA FROM ROUTINE STATIONS (surface only)

Month	Stations							
	20—1		24—1·5		24—1		28—1	
	T °C	O_2 cc/L	T °C	O_2 cc/L	T °C	O_2 cc/L	T °C	O_2 cc/L
August	12·39	5·71	13·34	7·19	13·09	—	13·56	5·60
September	13·49	6·09	13·61	7·17	13·56	—	14·70	6·31
October	13·99	7·66	12·64	7·94	12·90	—	12·29	6·51
November	13·47	6·16	9·83	2·71	13·22	—	14·56	7·72
December	—	—	12·89	6·56	12·79	—	13·29	6·49
January	15·05	6·40	15·07	5·72	15·07	—	13·53	7·71

red water and other points of interest.

Hydrological observations including temperature, salinity, oxygen and current data made in the St. Helena Bay area by the ships of the Division of Sea Fisheries on their routine cruises, provided useful environmental information.

In addition, special hydrological samples of temperature, oxygen and certain trace elements were taken at points where the red water samples were collected.

Information about the red water and associated phenomena was obtained from local residents at Lamberts Bay, Elands Bay, Laaiplek, Stompneus Bay, Ysterfontein and Melkbos. Only uncontradicted statements from more than one independent observer were recorded. Despite these precautions, however, such observations must be accepted with caution.

HYDROGRAPHIC CONDITIONS

The surface temperatures for the St. Helena Bay routine Stations (20-1, 24-1, 24-1·5) and the Station off Cape Columbine (28-1) between August 1966 and January 1967 are given in Table I. A comparison of the average sea-surface temperature for the spring and summer periods during the years 1963-1965 with those of the same seasons in 1966/67, showed that during the latter period the average temperatures were considerably lower than those of the previous years. This probably indicated more intense upwelling.

From Table 1 it is seen that the temperatures at Station 24-1·5 were lower from October to December, and were very low in November. This low temperature suggests that strong upwelling occurred in St. Helena Bay in November, and preceded the red water bloom. During the red water outbreak, the surface temperature was unusually high for this area, being 17·5°C off Elands Bay on 21 December (Table II). Only a short distance off the beach in the green water, however, the temperature was 14·0°C.

The surface oxygen values for the routine Stations from August 1966 to January 1967 are given in Table I. At Station 24-1·5 the oxygen value was exceptionally low in November, and this also demonstrated the probability of strong upwelling in St. Helena Bay. In December, the water at that station was supersaturated with oxygen which may well have been due to high photosynthetic activity in that area.

The high oxygen values (Table II) of the red water samples also suggest photosynthetic activity and confirm that the red water was alive and active even after the marine fauna mortality. There was no evidence of oxygen depletion which would be caused by decaying plankton.

Concentrations of the trace elements such as copper, iron and manganese, fell within the expected range for this area, and there is no evidence that abnormalities in concentrations of these elements played any part in the generation of the red water bloom. (Table II).

Three-hourly wind data for December 1966 from Cape Columbine lighthouse (Fig. 2) showed that during the first half of December there were strong southerly and south-easterly winds. About 16 December, the wind swung round to the north-west and from 18 to 22 December it was mainly calm at Elands Bay, with intermittent light south-westerly or

TABLE II: HYDROLOGICAL DATA FROM RED WATER STATIONS

Date	Station	Surface-Temperature (°C)	Oxygen (cc/L)	Trace Elements		
				Copper (μg/L)	Iron (μg/L)	Manganese (μg/L)
21/12/1966 ..	Elands Bay — 1 and 2	17·5	5·32	2·7	10·6	3·4
21/12/1966 ..	Elands Bay — 3	14·0	6·90	1·0	6·2	3·2

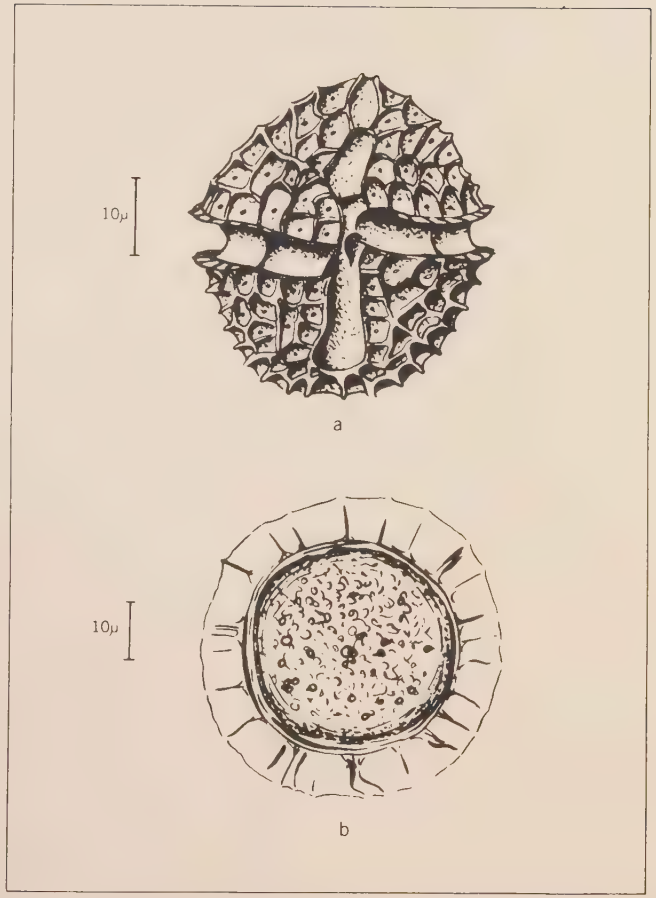

FIG. 5. GONYAULAX GRINDLEYI (a) VENTRAL VIEW OF ADULT THECA, (b) CYST SHOWING SPINES ENVELOPED BY MEMBRANE

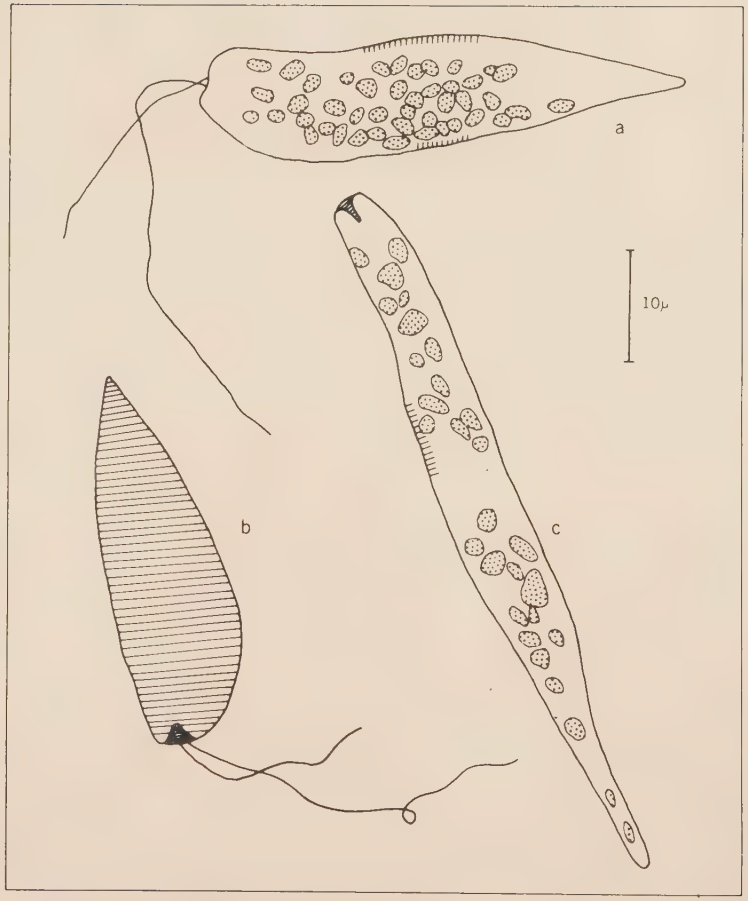

FIG. 6. EUTREPTIELLA sp: GENERAL VIEW SHOWING (a) TWO FLAGELLA AND CHROMATOPHORES (b) STRIAE AND CONCAVE DEPRESSION AT BASE OF FLAGELLA, (c) ANOTHER LONGER INDIVIDUAL

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north-westerly on-shore breezes. These breezes concentrated the red water in shore. Comparable conditions have been found to cause red water blooms in many other parts of the world (Brongersma-Sanders 1957; Grindley & Taylor 1964; Ryther 1955). From 26 December to the beginning of January, strong southerly winds prevailed again and dispersed the bloom off shore.

From Figure 4 it is also seen that the fauna mortality occurred at Elands Bay after the wind had changed to a northerly direction, and had concentrated the red water in shore.

During the major part of December, the weather was fine, with hot sunny days. From 10 to 12 December, it was overcast, but then cleared and remained fine until the 20th. Sunny weather combined with calm conditions before a red water outbreak helps to increase the surface temperature in the area, and these factors are known to be important in causing red tides (Ryther 1955; Brongersma-Sanders 1957; Grindley & Taylor 1964).

RESULTS

Occurrence of red water

The red water outbreak which was present during the second half of December 1966, extended from a few miles south of St. Helena Bay to at least 50 miles northwards. The approximate area is shown in Figure 3.

The causative organism *Gonyaulax grindleyi* (Fig. 5a), is a small species lacking an apical horn or antapical spines, and possessing girdle lists. It does not form chains. The girdle is displaced about one girdle width. The closing plate is exceptionally large (Reinecke 1967). The theca has strongly developed reticulations and the cell contents are yellowish. A series of measurements taken of these cells showed that they were generally longer than broad, the length being 25-42 μ, and the width 24-42 μ.

The discolouration of the water was caused by very high concentrations of *Gonyaulax grindleyi*, and there was little other phytoplankton present at that time.

The phytoplankton associated with *Gonyaulax grindley* during the actual red water bloom are listed in Table III. Diatoms were the most common, only three species of Dinophyceae occurring at the same time as *Gonyaulax*. Two small species of Tintinnids also appeared in these samples, one of which *Tintinnus pectinis* was present in small numbers in all the red water samples. The diatoms were never found in large numbers, and the most common were *Cocconeis* spp., *Navicula* spp. and *Thalassiosira* spp.

Apart from the cells of *Gonyaulax grindleyi*, two other species of dinoflagellates occurred in fair numbers in the samples. One was a small Euglenoid form *Eutreptiella* sp.* that was present in all the December samples, the cell counts ranging from 45,000-835,000 cells/litre (Fig. 6). The other was an unarmoured dinoflagellate *Gyrodinium obtusum*,** that was only found in the four samples (4, 5, 6, 7) taken in a straight line from the beach seawards, the cell counts being 30,000-132,500 cells/litre (See Figure 7).

Table III: Phytoplankton associated with *Gonyaulax grindleyi*

DIATOMS
- *Actinoptychus undulatus*
- *Biddulphia pulchellum*
- *Chaetoceros decipiens*
- *Cocconeis* species
- *Corethron criophilum*
- *Coscinodiscus gigas* var. *praetexta*
- *Coscinodiscus* species
- *Licmophora abbreviata*
- *Navicula* species
- *Nitzschia closterium*
- *Nitzschia delicatissima*
- *Nitzschia pungens* var. *atlantica*
- *Paralia sulcata*
- *Planktoniella sol*
- *Rhizosolenia hebetata* f. *semispina*
- *Rhizosolenia styliformis*
- *Rhoicosphenia* species
- *Thalassionema nitzschioides*
- *Thalassiosira decipiens*
- *Thalassiosira* species
- *Tropidoneis* species

OTHER SPECIES
- *Dinophysis* species
- *Eutreptiella* species
- *Gyrodinium obtusum*
- *Tintinnus pacificus*
- *Tintinnus pectinis*
- Ciliata (unidentified)

Spiny dinoflagellate cysts, presumed to be cysts of *Gonyaulax grindleyi* (Fig. 5b), also occurred in small numbers in the samples. Although they were counted separately from the *Gonyaulax* cells in samples 4, 5, 6 and 7 only, these cell counts may be taken as the average number of cells/litre in the other December samples as well (Table IV, VI).

Three counts of the number of cells/litre were done on each of the samples taken on 21 December at Elands Bay, that is samples 1, 2, 3, 4, 5, 6 and 7 (Fig. 1). The results are shown in Table IV.

Very high concentrations of *Gonyaulax grindleyi* were found in all these samples, except sample 3 which was taken in green water. In samples 1, 2 4, 5,

* Kindly identified by Professor T. Braarud of the University of Oslo, Norway.

** Kindly identified by Professor E. Balech of the Estación Hidrobiológica de Puerto Quequén, Argentina, and Professor E. J. Ferguson Wood of the Institute of Marine Science, University of Miami, Florida.

TABLE IV: COUNTS ON RED TIDE SAMPLES — ELANDS BAY, DECEMBER 1966

Species	Counts in Cells/Litre		
	1	2	3
Sample 1:			
Gonyaulax grindleyi	6,667,500	6,647,500	6,210,000
Eutreptiella species	540,000	552,500	610,000
Tintinnus pectinis	5,000	10,000	12,500
Navicula species	5,000	2,500	2,500
Cocconeis species	—	2,500	2,500
Licmophora abbreviata	2,500	—	—
Thalassiosira decipiens	2,500	—	—
Total	7,222,500	7,215,000	6,837,500
Sample 2:			
Gonyaulax grindleyi	5,555,000	5,547,500	5,587,500
Eutreptiella species	375,000	447,500	400,000
Tintinnus pectinis	—	7,500	5,000
Tintinnus pacificus	—	—	2,500
Dinophysis species	—	—	2,500
Cocconeis species	—	2,500	—
Coscinodiscus species	5,000	—	—
Total	5,935,000	6,005,000	5,997,500
Sample 3:			
Gonyaulax grindleyi	667,500	505,000	640,000
Eutreptiella species	45,000	57,500	140,000
Thalassiosira decipiens	—	5,000	10,000
Cocconeis species	—	—	2,500
Navicula species	—	—	2,500
Nitzschia closterium	2,500	—	—
Tintinnus pectinis	—	2,500	2,500
Total	715,000	570,000	797,500
Sample 4:			
Gonyaulax grindleyi	5,845,000	6,582,500	5,982,500
Eutreptiella species	835,000	802,500	795,000
Gyrodinium obtusum	30,000	52,500	35,000
Tintinnus pectinis	7,500	12,500	7,500
Thalassiosira species	10,000	15,000	7,500
Cysts of *Gonyaulax grindleyi*	—	—	7,500
Cocconeis species	—	5,000	—
Navicula species	—	2,500	2,500
Nitzschia delicatissima	—	5,000	—
Rhoicosphenia species	2,500	—	—
Tropidoneis species	2,500	2,500	2,500
Total	6,732,500	7,480,000	6,840,000
Sample 5:			
Gonyaulax grindleyi	5,420,000	5,135,000	5,047,500
Eutreptiella species	580,000	552,500	500,000
Gyrodinium obtusum	45,000	52,500	55,000
Tintinnus pectinis	17,500	7,500	2,500
Cysts of *Gonyaulax grindleyi*	—	2,500	2,500
Coscinodiscus species	—	2,500	—
Ciliata (various)	—	2,500	—
Total	6,062,500	5,755,000	5,607,500

Species	Counts in Cells/Litre		
	1	2	3
Sample 6:			
Gonyaulax grindleyi	5,730,000	5,782,500	6,145,000
Eutreptiella species	370,000	435,000	392,500
Gyrodinium obtusum	132,500	92,500	117,500
Tintinnus pectinis	12,500	5,000	15,000
Cysts of *Gonyaulax grindleyi*	—	2,500	2,500
Thalassiosira decipiens	5,000	—	—
Thalassiosira species	2,500	2,500	5,000
Planktoniella sol	—	—	2,500
Rhizosolenia styliformis	—	2,500	—
Tropidoneis species	2,500	—	—
Ciliata (various)	2,500	—	—
Total	6,257,500	6,322,500	6,680,000
Sample 7:			
Gonyaulax grindleyi	5,722,500	5,592,500	5,485,000
Eutreptiella species	395,000	440,000	332,500
Gyrodinium obtusum	75,000	90,000	90,000
Tintinnus pectinis	5,000	12,500	7,500
Cysts of *Gonyaulax grindleyi*	5,000	5,000	5,000
Thalassiosira species	5,000	2,500	—
Thalassionema nitzschioides	—	—	5,000
Rhizosolenia hebetata f. *semispina*	—	5,000	—
Nitzschia delicatissima	—	2,500	—
Nitzschia pungens var. *atlantica*	2,500	—	—
Cocconeis species	—	2,500	—
Ciliata (various)	—	2,500	—
Total	6,210,000	6,155,000	5,925,000

6 and 7, the cell counts ranged from 5,047,500 - 6,667,500 cells/litre, whereas they were about ten times less in sample 3 (Table IV).

On 5 January, when the red water was dispersed by the off-shore winds, four water samples were taken at places within the area of the red water outbreak, namely samples AI, AII, AIII and AIV (Fig. 2). The cell numbers for the species present in these samples are given in Table V.

Table VI shows the relative numbers of *Gonyaulax grindleyi* in the different samples. From this it can be seen that this species formed 87-93% of the phytoplankton in the December samples, and only 9·8% and 10·2% of the January samples from Elands Bay and Lamberts Bay respectively, while it was completely absent in the waters at Laaiplek and Stompneus Bay at this time. *Eutreptiella* sp. formed 6·3% to 11·7% of the December samples, but was completely absent in January.

Qualitative examination of the samples taken in December and January at Ysterfontein, Melkbos, Blouberg, Sea Point and Muizenberg showed that no *Gonyaulax* was then present in those areas.

Occurrences of *Gonyaulax grindleyi* before the bloom

Analysis of the routine samples taken by means of a N50V and a Nansen-Pettersson water sampler from the West Coast revealed that *Gonyaulax grindleyi* first made its appearance in the plankton in September (Table VII). It was present in small numbers at Stations about five miles from the coast (Fig. 2) in the area from Cape Columbine (28-1) northwards to Lamberts Bay (20-1). In October it had disappeared from the plankton off Cape Columbine, but was found in larger numbers in St. Helena Bay, particularly at Station 24-1·5. In November more cells occurred off Lamberts Bay than in St. Helena Bay itself. In December, due to bad weather, the Lamberts Bay station was not occupied, so no routine data are available for that month. The samples from St. Helena Bay (24-1·5), however, contained large numbers of resting stages, but no *Gonyaulax* cells were observed in December before the bloom (Tables VII, VIII). The resting stages were obviously dinoflagellate spores. They were smaller than the cells of *Gonyaulax grindleyi,* non-reticulate and the cell contents were yellowish-brown. Figure 8 shows the two forms of resting stages observed, and also two of

TABLE V:—COUNTS ON SAMPLES FROM THE WEST COAST — JANUARY 1967

Species	Counts in Cells/Litre		
	1	2	3
AI — ELANDS BAY:			
Gonyaulax grindleyi	2,500	17,500	7,500
Cocconeis species	5,000	—	2,500
Grammatophora species	—	7,500	—
Navicula species	15,000	22,500	35,000
Nitzschia delicatissima	—	22,500	12,500
Nitzschia seriata	—	5,000	—
Paralia sulcata	—	10,000	20,000
Thalassiosira species	27,500	32,500	25,000
Triceratium favus	—	2,500	—
Helicostomella species	—	2,500	—
Metacylis species	—	—	2,500
Tintinnus pectinis	—	—	2,500
Total	50,000	122,500	107,500
AII — LAMBERTS BAY:			
Gonyaulax grindleyi	2,500	5,000	7,500
Biddulphia species	—	2,500	15,000
Cerataulina bergonii	—	—	5,000
Cocconeis species	2,500	—	—
Gyrosigma species	5,000	5,000	10,000
Navicula species	12,500	15,000	17,500
Paralia sulcata	32,500	—	—
Rhabdonema species	2,500	—	—
Thalassiosira species	—	—	2,500
Triceratium favus	—	2,500	—
Triceratium species	2,500	—	—
Total	60,000	30,000	57,500
AIII — LAAIPLEK:			
Cocconeis species	5,000	2,500	2,500
Coscinodiscus species	2,500	—	—
Grammatophora species	—	2,500	—
Gyrosigma species	2,500	5,000	2,500
Leptocylindrus danicus	5,000	—	7,500
Navicula species	2,500	57,500	25,000
Nitzschia species	32,500	37,500	47,500
Thalassionema nitzschioides	5,000	—	—
Tropidoneis species	10,000	27,500	20,000
Desmids	12,500	22,500	30,000
Total	77,500	155,000	135,000
AIV — STOMPNEUS BAY:			
Biddulphia pulchellum	15,000	—	—
Biddulphia species	—	12,500	32,500
Cocconeis species	7,500	5,000	—
Grammatophora marina	32,500	42,500	20,000
Navicula species	55,000	125,000	77,500
Rhabdonema species	5,000	5,000	10,000
Tabellaria species	—	2,500	—
Tropidoneis species	2,500	2,500	10,000
Desmids	15,000	32,500	7,500
Total	132,500	327,500	157,500

TABLE VI: MEAN RED WATER CELL COUNTS

Species	Red water Samples										
	1	2	3	4	5	6	7	AI	AII	AIII	AIV
nyaulax grindleyi	6,508,333	5,563,333	604,167	6,136,667	5,200,833	5,885,833	5,600,000	9,167	5,000	—	—
	91·8%	93·0%	87·0%	87·4%	89·5%	91·7%	92·1%	9·8%	10·2%		
sts of *Gonyaulax grindleyi* only counted separately in samples 4, 5, 6, 7)	—	—	—	2,500	1,667	1,667	5,000	—	—	—	—
treptiella sp.	567,500	407,500	80,833	810,833	544,167	399,167	389,167	—	—	—	—
	8·0%	6·8%	11·7%	11·6%	9·4%	6·3%	6·4%				
rodinium obtusum ..	—	—	—	39,167	50,833	114,167	85,000	—	—	—	—
an Total Cell Counts ..	7,091,667	5,979,167	694,167	7,017,500	5,808,333	6,420,000	6,096,667	93,333	49,167	122,500	205,833

TABLE VII: PHYTOPLANKTON SETTLED VOLUMES AT ROUTINE STATIONS

Month	Station	Settled Volume cc	Presence of *Gonyaulax grindleyi*
September 1966	20—1	45	Few
	24—1·5	235	Few
	28—1	88	Few
October 1966	20—1	126	Fair number
	24—1·5	54	Many
	28—1	12	—
November 1966	20—1	54	Fair number
	24—1·5	7	Few
	28—1	12	—
December 1966	24—1·5	375	Many dinoflagellate resting stages
	28—1	24	—
January 1967	20—1	18	
	24—1·5	21	(Few chains *Gonyaulax catenella*)
	28—1	51	—

TABLE VIII: NANSEN-PETTERSSON COUNTS FOR *Gonyaulax* CELLS AT STATIONS 20—1, 24—1·5, 28—1

Month	*Gonyaulax* cell counts in Cells/Litre		
	Station 20—1	Station 24—1·5	Station 28—1
September 1966	—	—	+ Dinoflagellate resting stages = 7,500
October 1966	+ *Gonyaulax grindleyi* = 10,000	+ Dinoflagellate resting stages = 2,500	—
November 1966	—	—	—
December 1966	Not done	+ Dinoflagellate resting stages = 15,000 *Gonyaulax catenella* = 10,000	—
January 1967	—	+ *Gonyaulax catenella* = 10,000	—

TABLE IX: MORTALITY OF MARINE FAUNA

Species	ELANDS BAY (Rocky shore)	ELANDS BAY (Sandy beach)	LAMBERTS BAY (Rocky shore)
COELENTERATA (Sea anemones)			
Bunodosoma capensis (Lesson)	+		
CRUSTACEA (Crabs and lobsters)			
Plagusia chabrus (Linn.)	+		
Jasus lalandii (M. Edw.) juveniles	++		
LAMELLIBRANCHIATA (Mussels)			+
Mytilus crenatus Lamarck			++
Chloromytilus meridionalis (Krauss)	+		++
Donax serra Röding		++++	
RHIPIDOGLOSSA (Winkles)			
Oxystele tigrina (Dillwyn)	+		
Oxystele variegata Anton	+		
Turbo samarticus Linn.	+		
RHACHIGLOSSA (Whelks)			
Bullia digitalis (Dillwyn)		++	
Bullia laevissima (Gmelin)		+++	
Burnupena cincta (Röding)			+
PATELLACEA (Limpets)			
Patella compressa Linn.	+		+
Patella granatina Linn.	+		++
Patella granularis Linn.			+
CEPHALOPODA (Squids and Octopus)			
Eledone species	++		
HOLOTHURIA (Sea cucumbers)			
Cucumaria frauenfeldii Ludwig	++		
Thyone aurea Quoy & Gaimard	++		
PISCES (Fish)			
Chorisochismus dentex Bloch	+		

Numbers observed: + = 1—10; ++ = 11—100; +++ = 101—1,000; ++++ = 1,000+.

these which appeared to be attached. The general body shape as well as the chain formation of the resting stages suggests that these were stages of *Gonyaulax catenella*. By January, *Gonyaulax grindleyi* had disappeared from the plankton in that area (Table VII).

As *Gonyaulax grindleyi* was not present in large numbers in the St. Helena Bay plankton before the red water outbreak, it was not very common in the Nansen-Pettersson samples taken at 10 m. Table VIII gives the counts of *G. grindleyi* cells from these samples. From this table it can be seen that cells of *G. grindleyi* were present in water-bottle samples taken off Lamberts Bay during October. Dinoflagellate resting stages were present off Cape Columbine in September and in St. Helena Bay during December.

A few chains of *Gonyaulax catenella*, not previously recorded from the West Coast of South Africa, were observed in the samples taken in December and January at a depth of 10 m in St. Helena Bay. This species is well known as the cause of mussel poisoning along the California Coast (Sommer & Meyer 1937). Although it was not present in the red water samples, it is possible that *G.* catenella was the organism responsible for the mussel poisoning along the West Coast of South Africa from December 1966.

Table VII gives the phytoplankton settled volumes (N50V net samples) and the presence of *Gonyaulax grindleyi* at the three routine Stations from September 1966 to January 1967. High phytoplankton volumes were present in September and December in St. Helena Bay and also in October at Lamberts Bay.

Mass Mortality

The red water outbreak resulted in the death of a large number of White and Black mussels, as well as other marine fauna. The greatest mortality of these invertebrates occurred at Elands Bay (Fig. 1), and a list of the dead animals is given in Table IX. It is interesting that almost no fish died during the outbreak, and only a few sucker-fish *Chorisochismus dentex* were washed ashore.

It was not clear what mechanism was involved in the death of these marine invertebrates. There was no evidence of a mass decay of plankton, such as occurred in False Bay in 1962 (Grindley & Taylor 1964). There was no slime or smell of rotting plankton and the sea remained luminescent at night throughout the period, while plankton samples contained large numbers of living *Gonyaulax grindleyi* and only few cysts or decaying cells, indicating that the plankton was alive. The mortality could thus hardly have been caused by the mass decay of plankton depleting the oxygen in the water.

It seems probable that the mortality of marine invertebrates in this case was due either to mechanical clogging of the gills of the affected organism or to a specific toxin. Most of the animals killed by the red water had very fine filamentous gills. Examination of the gills and gut contents of dead mussels from the affected area showed that while there were many *Gonyaulax* cells on the gills, there were no identifiable *Gonyaulax* cells in the gut contents, although some unidentified red-pigmented material was present.

The species composition of the invertebrate organisms killed by the red water (Table IX) was somewhat similar to that found at Gordons Bay in 1962 (Grindley & Taylor 1964). However, the scale of the mortality and the number of affected species was much smaller in the present case; the almost complete absence of fish is particularly noteworthy. The vast majority of organisms killed were adult White mussels and only two other species appear to have been affected on the sandy beach which formed most of the affected area (Table IX). Certain organisms seemingly escaped the mortality, namely *Littorina capensis, Siphonaria sp., Patella granularis* (which occurs high on the shore) and juvenile *Donax serra* which are also found some distance from the waters edge.

Paralytic shellfish poisoning

Toxicity tests carried out on mussels collected from the affected area during December revealed that both White and Black mussels, including live specimens, were highly toxic.

Mussels gathered during December from Lamberts Bay, Elands Bay, Laaiplek and Stompneus Bay (Fig. 3) within the area of the red water, were all found to be toxic, as were also the Black mussels from Ysterfontein and the White mussels from Paternoster, both these areas being south of the red water outbreak. Other mussels examined from Strandfontein, Saldanha Bay, Melkbos, Blouberg, Sea Point and Muizenberg were all found to be non-toxic.

Attempts were made to extract the toxin directly from the cells of *Gonyaulax grindleyi* but the results were negative. 900 ml of red water from Elands Bay, containing approximately 5,400,000 cells of *Gonyaulax grindleyi* were centrifuged, and the resultant centrifugate weighted about 100 mg. An extract was prepared and injected intraperitoneally into two standard 20 g white mice. No neurological symptoms, however, appeared in either mouse.

It is known that a centrifugate of equal weight of *Gonyaulax catenella* would yield 1,000 mouse units of toxin, sufficient to kill approximately 1,000 mice (Halstead 1965). Far lower toxicities would be detectable even by the simple test of Sommer & Meyer (1937) employed here, thus it would appear

TABLE X: TOXICITY OF BLACK AND WHITE MUSSELS

Place where Mussel sample taken (Listed from North to South)	Type of Mussel Tested for Toxicity	Toxicity Results Date when Sample taken — 1966-67 Dec.	Jan.	Feb.	March	April	May	June
STRANDFONTEIN .. .. .. (± 40 miles North of Lamberts Bay)	Black	—		—				
	White	—						
LAMBERTS BAY	Black	×	—		—			
ELANDS BAY	Black	×	×		×		—	—
	White	×	×		×	×		—
DWARSKERSBOS	Black		—					—
	White					×		×
LAAIPLEK	White	×						
STOMPNEUS BAY	Black	×						
PATERNOSTER	White	×	×		—			×
SALDANHA BAY	Black	—		—				
	White	—		—				
YSTERFONTEIN	Black	×	×					
MELKBOS	Black	—		—				
	White	—		—			×	
BLOUBERG	White	—		—				
SEA POINT	Black	—						
MUIZENBERG	White	—						

× = Toxic.
— = Non-toxic.

White mussels = *Donax serra* Röding
Black mussels = *Mytilus crenatus* Lamarck
Chloromytilus meridionalis (Krauss)

that *Gonyaulax grindleyi* does not produce toxins of the mussel-poison type.

Although the *Gonyaulax* cells had disappeared from the plankton by the end of January (Table VII), the mussels were still found to be toxic for months afterwards. The mussels concentrate the toxin in their digestive glands, and Needler (1949) found that the toxicity builds up as the shellfish feed on the toxic plankton, and that it disappears slowly after the cause is removed.

The results of the toxicity tests on the Black and White mussels are given in Table X. In December 1966 tests were made on both dead and live mussels, but from January 1967 after the mass mortality, only live specimens were tested. From this it is seen that Black mussels from Elands Bay, which had the largest red water concentration and mass mortality, were toxic until March 1967 and White mussels until April 1967.

Mussels from Laaiplek and Stompneus Bay were not tested after December, but mussels samples from Dwarskersbos, about 7 miles north of Laaiplek, were tested from January onwards. The Black mussels were found to be non-toxic, but the White mussels were toxic in April and June (Table X).

Although the Benguela Current flows from south to north along the West Coast of South Africa, Duncan & Nell (in press) have found from drift card returns that in summer there is a counter current flowing in a southerly direction close in shore. This current probably carried the *Gonyaulax* cells southwards along the coast, as some of the places where mussels were found to be toxic were well south of the St. Helena Bay area (Fig. 3). As the mussels concentrate the toxin, large numbers of the toxic plankton organisms need not be present.

Mussels from Lamberts Bay were non-toxic from January onwards (Table X).

Toxicity tests on White mussels from Paternoster showed that these mussels were still toxic in January and even in June 1967. Ysterfontein Black mussels were still toxic in January.

Mussels from Melkbos which is far south of the red water outbreak, were non-toxic in December and February, but White mussels were very highly toxic in May 1967 (Table X).

As Black mussels form an important part of the diet of the Cape rock-lobster *Jasus lalandii* which in turn is widely eaten by man, it was desirable to examine rock-lobsters for toxicity. Rock-lobsters from Lamberts Bay, Elands Bay and Sea Point were tested but only those from the first two localities, that is within the red water area, contained any toxin.

From the results it seems that mussel poison is not taken up by the bodies of the lobsters but may appear in the proventriculus, presumably in the form of undigested portions of mussel. The tail of the rock-lobster which is the part usually eaten by man, is unaffected.

FIELD OBSERVATIONS AND INTERVIEWS

Elands Bay, 21/12/1966

Dense patches of dark red water extended in all directions. In the afternoon the wind, which changed to fresh south-westerly, dispersed the red water. Local fishermen confirmed that the marine fauna mortality had occurred on the previous day and reported that red water first appeared in shore on 17 December. Fishing was normal, but the rock-lobsters were very close in-shore. Masses of marine invertebrates lay dead amongst the rocks and large numbers of dead White mussels and whelks were scattered along the high-water mark on the sandy beach. The red water was composed of living organisms, as it was strongly luminescent at night.

Elands Bay, 5/1/1967

The hotel manager and local fishermen confirmed that red water had only been dense for about five days. They reported that it occurred quite frequently in that area, and although a few shellfish were sometimes killed and washed onto the beach, the 1966 mortality had been the greatest over the past ten years. The White mussels were washed up along the beaches for about five miles to the north, and the only dead fish were a few suckerfish *Chorisochismus dentex*. According to local fishermen, patches of red water had first drifted in with the wind from the west, and had remained luminescent at night throughout the period. The local people never eat Black or White mussels, and were not aware of any case of mussel poisoning.

Lamberts Bay, 5/1/1967

A few dark-red patches were visible off the harbour, but the water in shore was clear. There was still evidence of marine fauna mortality. A factory manager and the skippers of some fishing boats confirmed that there had been red water and phosphorescence at night for about a week before Christmas, that is about 18-24 December. There had been a slight mortality of marine fauna including mussels and other shellfish, also some klipfish and a few rock-lobsters. The weather had been calm and hot during this period with only slight on-shore north-westerly breezes. Apparently the red water occurs in that area almost every year at about the same time, and although local residents were not aware of any cases of mussel poisoning, nobody there ate mussels. Skippers of fishing boats reported that the red water had extended more than eight miles to

the north of Lamberts Bay. About two years before a few people who had eaten fish caught in the red water, had become ill afterwards.

Laaiplek, 5/1/1967

Local fishermen and construction workers confirmed that there had been some red water in that area before Christmas, but that it had not been very dense, and that there had been no noticeable mortality of marine fauna. Local people did not eat mussels.

Stompneus Bay, 5/1/1967

Red water was present in small concentrations before Christmas, but had become more dense between Christmas and New Year, that is between 25-31 December 1966. The red water had drifted around the Point and southwards past Paternoster during the latter period.

Ysterfontein, 24/1/1967

The sea was brownish and discoloured, but examination showed that this was only due to diatoms and detritus. Local anglers reported that they had not seen any red water in December or January, although the sea had been very "dirty" around New Year. They did not eat mussels.

Melkbos, 24/1/1967

No red water was seen in December or January. Local people had heard of mussel poisoning (probably the 1948 case at Blouberg) and they did not themselves eat mussels.

DISCUSSION

A number of factors have been suggested by different authors as being the cause of red tides. Rounsefell & Nelson (1966) who were mainly concerned with the Florida red tides caused by the dinoflagellate *Gymnodinium breve,* have discussed the significance of some factors in other localities.

High surface temperature. Dinoflagellates as a group favour warm water, and are generally more abundant near the surface. This does not necessarily mean that they only occur in warm seas, as the surface of the sea in normally cool areas may be warmed up during periods of hot, calm weather.

Wind. A strong off-shore wind aids upwelling, while a gentle on-shore wind concentrates the bloom near the coast. On the other hand, heavy weather and strong winds disperse the bloom.

Light intensity. Most of the organisms responsible for the red tides are dependent on light. A period of bright, sunny, calm weather before the outbreaks has often been noticed.

Nutrients. All authors agree that red tides usually occur after upwelling has stopped, and that the nutrients brought to the surface do not themselves appear to be the direct cause of these blooms. It is thought that the preceding blooms of diatoms may impoverish the water and reduce one or more of the inorganic nutrients to a level favourable for the growth of dinoflagellates, and also allow the production of organic nutrients such as Vitamin B_{12} which are important to their growth.

Ryther (1955) lists red water outbreaks in different parts of the world, and the ecological conditions preceding or accompanying outbreaks. He summarizes the basic requirements for an outbreak of red water as a seed population of dinoflagellates, and the existence of favourable conditions for the growth of one or more species. As regards favourable conditions, he mentions high surface temperature, reduced nutrients after a diatom bloom, calm weather before the outbreak and on-shore winds which concentrate the bloom.

The environmental conditions present in the vicinity of Elands Bay before and during the red water outbreak agree with those mentioned above. *Gonyaulax grindleyi* was present in small numbers in the plankton of the St. Helena Bay area from September. In November the low surface temperature and the low oxygen value inferred that strong upwelling had occurred in that area (Table I). This was followed by high phytoplankton blooms (Table VII), as demonstrated by the high oxygen values and the settled volumes of phytoplankton during December. A large bloom of phytoplankton in October off Lamberts Bay may also have helped to reduce the nutrient concentrations to a level favourable for the bloom of *Gonyaulax grindleyi,* because in November there were more *grindleyi* cells off Lamberts Bay than at Station 24-1·5 (Table VII). *Gonyaulax grindleyi* which were present in fair numbers in St. Helena Bay in October, probably either encountered unfavourable conditions after the upwelling in that area during November or the cells were blown in shore; this would account for the absence of cells off shore in the routine samples taken in December.

After the disappearance of strong winds that had prevailed during the first part of December, there was a period of hot, calm, sunny weather favourable for the growth of dinoflagellates. The gentle in-shore westerly winds from 16 December concentrated the red water in shore (Fig. 4), and the mass mortality only occurred from 19 December.

Strong southerly off-shore winds dispersed the bloom later in the month.

Mussels surveyed at Elands Bay from 24-26 January showed how the population had been affected by the red water outbreak. A previous survey had been carried out during October 1966. Three transects done in January showed that no White mussels occurred from the low-water mark to approximately 30-40 feet above this tide mark. Spot checks were carried out above and below the high- and low-water marks. All these tests proved to be negative. This meant that the adult population of White mussels was completely annihilated, leaving only a belt of juveniles further up the beach. Thus, due to the red water, the White mussel population at Elands Bay suffered a severe blow, there being a decline of 68·8% in the total number of White mussels found in January compared with those from the October survey.

The relatively low incidence of mussel poisoning on the West Coast of South Africa is probably related to the unpopularity of mussels as a food (as revealed by the interviews). It is not yet certain what species of dinoflagellate is the source of the toxin. Sapeika (1948) discussed the nature of the poison, which is similar to that of *Gonyaulax catenella*. However, the pharmacological action of the toxin derived from various species of dinoflagellates is known to be similar (Sapeika 1953).

From all previous records of mass mortality and paralytic shellfish poisoning, it appears that the two phenomena are distinct, and have separate and different causes. It is interesting in this regard that both mass mortality of marine fauna and mussel toxicity occurred at Elands Bay, suggesting either the action of two different species, or that the same species was responsible for both phenomena. *Gonyaulax grindleyi* was seemingly the cause of the fauna mortality, due to the mechanical clogging of the gills. As there was no other species of *Gonyaulax* in the actual red water samples, the cause of the toxin in mussels is actually not known and cannot reasonably be assumed to be *Gonyaulax catenella* from just a few cells present in the routine samples. However, if the resting stages found in the routine samples from St. Helena Bay were indeed stages of *Gonyaulax catenella*, these may well have been the source of the poison. Further investigations into the annual red water blooms at Elands Bay may clarify this point and establish precisely which dinoflagellate is the source of mussel toxin on the West Coast of South Africa.

The fact that the mussels south of the affected area were also toxic can be correlated with the results of drift card releases, which showed the presence of an in-shore, southwards-moving counter current in the summer. As this current is between the coast and the routine Stations (which are 5-10 miles off the coast) one would not expect to find *Gonyaulax* cells at the routine Stations further south, as was indeed the case. However, the current probably carried these toxic cells south of the affected area, and they may then have been concentrated along the coast by on-shore winds. It is interesting that the White and Black mussels at Melkbos, which is about 170 miles south of Elands Bay, were non-toxic in December and February, but were very highly toxic in May (Table X). The mussels at Ysterfontein and Paternoster, also south of the red water area, but north of Melkbos were toxic earlier in the year (Table X). This was probably due to the rate of flow of the in-shore current and the prevailing wind at that time. In the affected area at Elands Bay, however, all toxicity had disappeared after four months (Table X).

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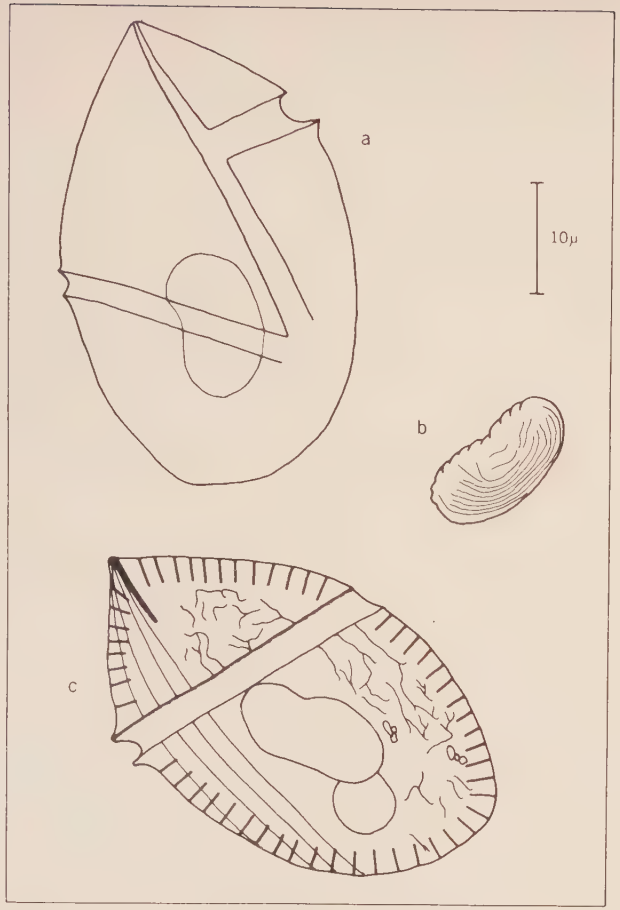

FIG.7. GYRODINIUM OBTUSUM: (a) VENTRAL VIEW SHOWING SULCUS AND SPIRAL GIRDLE, (b) NUCLEUS, (c) DORSAL VIEW SHOWING SLANTING GIRDLE, POSITION OF NUCLEUS AND SPHERICAL BODY, RIDGE ON EPICONE, RHABDITES AND SURFACE STRIAE.

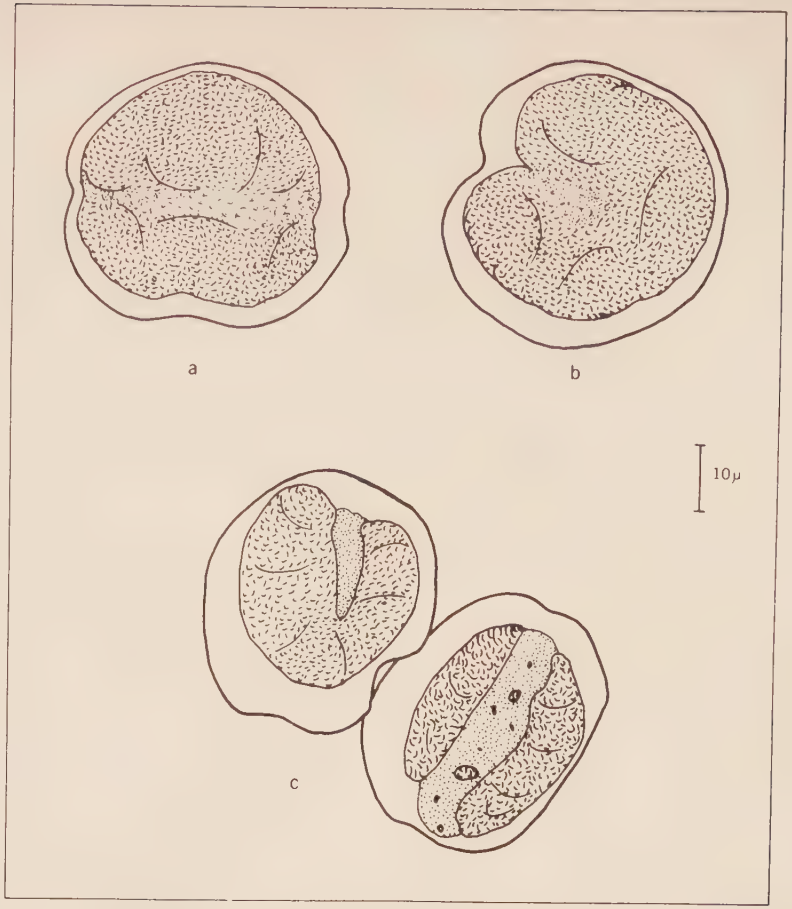

FIG.8. DINOFLAGELLATE RESTING STAGES: (a) VENTRAL VIEW SHOWING GIRDLE CONSTRICTIONS, (b) POLAR VIEW, (c) TWO RESTING STAGES SHOWING CHAIN FORMATION.

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